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Osteology of *Pedionomus torquatus* (Aves: Pedionomidae) and its Allies

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Abstract

The skeleton of *Pedionomus* is described and compared with those of *Turnix* and *Ortyxelos*. *Turnix* and *Ortyxelos* are quite similar to one another in most features of their skeleton, but are quite different from *Pedionomus* in many characteristics of the skull, sternum, pectoral girdle, wing and synsacrum. Only the elements of the hind limb are similar in these genera. The osteological evidence supports the current taxonomic status of *Turnix* and *Ortyxelos* as separate genera in the family Turnicidae. In view of the distinction of *Pedionomus* it is suggested, as a practical taxonomic conclusion, that the general practice of placing *Pedionomus* in a separate family, the Pedionomidae, be maintained. Several aspects in the definitions of palate and nostril types are discussed with the conclusion that the members of the Turnices possess a schizognathous palate and a schizorhinal nostril.

Introduction

The endemic Australian Plain-Wanderer (*Pedionomus torquatus*) has been known to science for over 100 years, yets its morphology is still little studied and its exact affinity with other birds remains disputed. The only anatomical study of this bird, to our knowledge, is the short contribution by Gadow (1891) which forms the basis of all subsequent taxonomic conclusions (but see Appendix 2). Gadow concluded (1891 : 211) that *Pedionomus* should be placed in the Turnices, a suborder of the Gruiformes that includes the Turnicidae (Button quails). Opinion differs on the closeness of relationship between the Pedionomidae and the Turnicidae. Mayr and Amadon (1951) believe that these taxa are distinct only on the subfamilial level, whereas Stresemann (1927-34: 760) and Wetmore (1960: 11) believe that these birds are more distinct and should be placed in separate families. Most classifications follow the latter course. Yet none of these opinions have any solid foundation because of the lack of comparative analyses of anatomical and other pertinent taxonomic characters.

A major reason for the lack of anatomical studies of *Pedionomus* is the rarity of anatomical specimens of this bird; no skeletons exist, to our knowledge, in any American or European museum. Lowe (1923: 279) makes the same observation on the rarity of specimens of many problem genera in the introduction of his study on the turnicid genus *Ortyxelos*. Hence, we seized upon the opportunity of McEvey's stay in New York to undertake an investigation of the skeletons of *Pedionomus* in the collections of the National Museum of Victoria. Although we shall focus attention in this study on the osteology of *Pedionomus*, the details of

the morphology of *Turnix* and of *Ortyxelos* cannot be overlooked. Excellent studies of the skull (and post-cranial skeleton, partly) of *Turnix* are available (Huxley 1867, 1868; Parker 1863, 1866, 1868, 1875), and the skull and several elements of the post-cranial skeleton of *Ortyxelos* were described (some parts very briefly) by Lowe (1923); yet a detailed analysis of the skeleton of these genera is not available as a basis for comparison with that of *Pedionomus*. The goal of this study is to present a comparative description of the skeletons of *Pedionomus, Turnix* and *Ortyxelos* as a foundation for further taxonomic work. The time available to us did not permit comparison of the osteology of these birds with other members of the Gruiformes and related orders.

The African genus *Ortyxelos* deserves a word of introduction. This bird was originally and correctly described by Vieillot as a member of the genus *Turnix* and shortly thereafter placed in a monotypic genus *Ortyxelos* by the same author. However, many subsequent workers believed it to be related to the shorebirds in the broadest sense and placed it in one or another family within the Charadriiformes in many works; *Ortyxelos* cannot be found under the Turnicidae in most studies published in the last century. Sharpe included it in the Glareolidae (his Cursoriidae) in his 'Catalogue of Birds in the British Museum' (Vol. 24). Lowe (1923), after a comparative study of the skeleton, reassigned *Ortyxelos* to the Turnicidae, a conclusion that has been followed by Peters in his 'Check-list' and by most other subsequent workers. We accepted Lowe's conclusion as a working hypothesis at the onset of our study and concurred with it ever more strongly as our work proceeded. The spelling of the generic name of this hemipode must also be clarified. The original and correct spelling is *Ortyxelos* used by Vieillot and followed by Peters (1934: 149) in his 'Check-list'. For reasons unknown to us, this name has been emended to *Ortyxelus* and is so used by Sharpe in his 'Catalogue' (Vol. 24), Lowe (1923), Stresemann (1927-34: 759-760, who uses both spellings), Wetmore (1960) and many other authors. We are not aware of any valid reasons for this emendation and would urge that the spelling of *Ortyxelos* be followed.

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Materials and Methods

The following skeletons were available and used in this study: *Pedionomus torquatus*, three complete specimens (National Museum of Victoria: W6084; W6655; W6698; these specimens were thoroughly cleaned, bleached and disarticulated); *Ortyxelos meiffrenii*, two partly damaged specimens (British Museum, Natural History: S/1952.2.71; S/1956.22.1; these specimens were thoroughly

cleaned and disarticulated; only the mandible, upper jaw and parts of the bony palate were lacking from these specimens which are the same ones studied earlier by Lowe); *Turnix sylvatica*, three complete specimens (U.S. Nat. Mus.: 344362; 344365; 429078); *T. tanki*, one complete specimen (Amer. Mus. Nat. Hist.: 1581); *T. suscitator*, one complete specimen (U.S. Nat. Mus.: 347288); *T. nigricollis*, two complete specimens (Amer. Mus. Nat. Hist.: 1944; 5381); *T. varia*, one complete specimen (Amer. Mus. Nat. Hist.: 1601); and *T. pyrrhothorax*, skull and mandible (National Museum of Victoria: 665). No special care was taken to obtain specimens of all species of *Turnix* although we did try to include representatives of larger species such as *varia* and heavy-billed forms such as *pyrrhothorax*.

Observations and drawings were made with the assistance of a stereo dissecting microscope. A Wild M5 microscope equipped with a drawing tube (camera lucida) was used for the drawing of all figures; care was taken to use the centre of the field to reduce the amount of spherical aberration which occurs at the edge of the field.

Terminology for the parts of the skull follows general standard usage and in particular follows the usage in earlier papers by Bock. (The reader is referred to Appendix 1 for a clarification of earlier usage of basipterygoid and basitemporal articulation.) Terminology for the parts of the post-cranial skeleton follows Howard (1929) with the addition of a few terms for structures not covered by Howard's terminology.

Description

In all descriptions of the skeleton, the bony elements of *Pedionomus* will be described first, followed by a description of *Turnix* and a briefer description of *Ortyxelos* only when it differs sufficiently from *Turnix*. A comparison of the bony element of the three genera follows the description. Because *Ortyxelos* and *Turnix* are similar in many parts of the skeleton, most of the comparison will be between *Pedionomus* and *Turnix*. The accompanying figures of each genus were drawn from favourable elements chosen from the available specimens to provide the most representative and accurate portrayal of the osteology. Some elements of *Ortyxelos*, notably the skull, were too badly damaged to figure. Reference should be made to Lowe (1923) who illustrated several bony elements of this genus.

THE SKULL AND LOWER JAW

PEDIONOMUS

BRAINCASE: The entire skull of *Pedionomus* (Fig. 1) is lightly built with the upper jaw depressed about 30° below the longitudinal axis of the basisphenoid rostrum. The braincase is high and wide but relatively short; the height is about three-quarters the braincase width, whereas the length is only half the width. In dorsal view, the posterior margin of the braincase is relatively flat with a small pointed projection just above the occipital plate. The supraorbital rims are narrow with a distinct median furrow between them; the furrow extends to the base of the upper jaw. No supraorbital grooves for nasal glands (absent in this bird?) exist. The width of the skull at the dorsal end of the lateral nasal bars (anterior limits of frontal) is equal to or just less than the width between the jugal bars. In lateral view, the anterior end of the supraorbital rim slopes down sharply to the base of the upper jaw. The orbit is quite large, about one-third the length of the skull, and the orbital septum is only partly ossified. A small postorbital process is present just

inside the lateral edge of the postorbital wall. Only the faintest suggestion of a temporal fossa exists on the lateral edge of the postorbital wall. An indistinct hollow is present on the postorbital wall just medial to the postorbital process and dorsal to the quadrate. A minute zygomatic process lies just above the squamosal articulation of the quadrate and again inside the lateral edge of the postorbital wall. A slightly larger suprameatic process lies ventral to the zygomatic process. A small, but distinct, suprameatic fossa lies at the bases of the zygomatic and suprameatic processes.

The occipital plate is elevated about 30° above the axis of the basisphenoid rostrum. The foramen magnum is large with the exact shape of its dorsoposterior margin depending upon the degree of ossification (presumably becoming rounder in older individuals). Moderate-sized auditory bullae flank the foramen magnum and the basitemporal plate; these bullae are solidly constructed, not thin walled shells as found in many birds. The basitemporal plate is flat with small lateral processes which are presumably capped, in life, with fibrous pads. The eustachian tube is expanded with a characteristically large opening above the lateral edge of the basitemporal plate and medial to the otic process of the quadrate. The basisphenoid rostrum is moderately inflated with small basipteryoid processes just anterior to the tip of the basitemporal plate.

Ectethmoid: The ectethmoid plate is rather small and rectangular in shape with a sharp ventrolateral projection; the ectethmoid does not project laterally beyond the outer limits of the lateral nasal bars. No ossifications attach to the anterior surface of the ectethmoid and the lacrymal is absent; the antorbital space, therefore, does not contain any ossifications. The ectethmoid foramen is single and large, extending almost to the lateral edge of the bone.

Upper Jaw: The upper jaw is just less than half the length of the skull and is straight with a slight dip at its tip. The nostril is large, extending about three-quarters the length of the upper jaw and is completely unossified. The posterior end of the nostril extends back just beyond the base of the upper jaw (schizorhinal), and is relatively wide and rounded. The ossified orbital septum extends forward slightly beyond the base of the upper jaw; hence, the skull is rhynchokinetic of the charadriiform type (Bock 1964a: 14-15). Close examination reveals that a flange of bone extends from the dorsal edge of the orbital septum to the lateral margin of the medial dorsal bar of the upper jaw. This flange lies just under the medial dorsal bar and a fraction can just be seen in the posterior end of the nostril (Fig. 1A).

Quadrate: The quadrate is low with its longitudinal axis inclined about 60° anterior to the vertical when the palate is in the resting retracted position. It has the usual double squamosal articulation with the medial facet on the squamosal slightly posterior and ventral to the lateral facet (Fig. 2). The dorsal head of the squamosal articulation lies between and is partly hidden by the zygomatic and suprameatic processes. These processes embrace the lateral half of the quadrate head between them. The orbital process of the quadrate is moderately short and broad, whereas the base is quite broad and short (in anteroposterior length). The lateral articular condyle and jugal articulation of the quadrate flare laterally as far as the lateral margins of the brain case. The articular condyles are flat with only the medial condyle projecting downwards as a distinct rounded knob. The posterior condyle lies between and behind the lateral and medial condyles as a distinct ridge extending from the lateral condyle.

Bony Palate: The pterygoid is a flat, broad and slightly twisted bone. It appears to be slightly bent at the basipterygoid articulation but this may be more apparent than real, resulting from the low process at the basipterygoid articulation. Both the pterygoid and palatine clasp the basisphenoid rostrum at their common articulation. However, the two lateral halves of the palate do not meet at any point along the midline. The palatine shelf that is concave ventrally, has a distinct posterolateral corner, short mediopalatine and interpalatine processes and a straight prepalatine bar (or process).

The exact structure of the vomer cannot be given with complete certainty. In all specimens, the vomer appeared to be limited to a pair of anterior processes extending from the anterodorsal corner of each palatine and lying along the basisphenoid rostrum (Fig. 1D); these correspond to the bars connecting the anterior plate of the vomer to the palatines in *Turnix* and other birds. No anterior medial ossification was seen attached to these processes in any specimen of *Pedionomus* available to us, and hence our initial conclusion was that the vomer is greatly reduced or absent in this genus. However, the anterior ossification of the vomer may be present but weakly attached to the posterior connecting bars and may fall off during preparation of the specimens. The skeletal specimens of *Pedionomus* were thoroughly cleaned and became extensively disarticulated during preparation. After careful search, a small bone was found with one specimen (N.M.V. W6084) that is most likely the anterior medial part of the vomer (Figs. 1E, 3). This bone is the right size and shape, and possesses long articular facets on its dorsal surface that correspond to the processes extending from the palatines. This bone does not correspond to any other element of the skeleton and we have identified it tentatively as the anterior ossification of the vomer. As such, the vomer is elongated, relatively narrow, has a slight ventral keel and has a pointed anterior tip. The tip of the vomer would extend anterior to the maxillo-palatines. The vomer is somewhat broader than in the typical schizognathous condition; however, it agrees closely with the basic characteristics of the schizognathous palate and not with the aegithognathous palate. Hence, we designate *Pedionomus* as a schizognathous bird.

Maxillo-Palatines: The jugals are thin and converge gradually and evenly from the quadrates to the base of the upper jaw. The jugal bar, prepalatine bar, lateral nasal bar and base of the maxillo-palatine pedicle meet at a common point at the ventral base of the upper jaw. The pedicle of the maxillo-palatine is fused to the dorsal surface of the prepalatine bar. The maxillo-palatine has a broad pedicle and an expanded flat tip that would cover much of the vomer when viewed from the ventral side.

Mandible: The mandible of *Pedionomus* (Figs. 1D, 8B and 9B) is slightly decurved without any prominent muscular attachments or articular surfaces except for a deep groove for the medial condyle at the base of the internal process. It has a characteristic double mandibular foramen. An external process just anterior to the articulation indicates that a postorbital ligament may be present. The retroarticular and internal processes of the mandible are short and broad; these processes are connected by a low posterior wall of the articular cavity. The internal process (Fig. 8B) articulates with the ventral tip of the lateral process of the basitemporal plate to form the secondary articulation (and brace) of the mandible (Bock 1960).

TURNIX

In addition to figuring the skull of *T. nigricollis* (Figs. 4, 8A and 9A) a typical member of the genus, we figure the skulls of *T. varia* (Fig. 6), which is one of the

largest members of the genus, and of *T. pyrrhothorax* (Figs. 5 and 9C), which possesses the heaviest bill in the genus and in the entire Turnices complex. The following description will be based upon the skull of *T. nigricollis* with reference to other members of the genus only on points of sufficient difference.

BRAINCASE: The entire skull of *Turnix* (Figs. 4, 5 and 6) is lightly built, although somewhat more solid than in *Pedionomus*, with the upper jaw depressed about 20° below the longitudinal axis of the basisphenoid rostrum. The braincase is lower, narrower and relatively long; the height is slightly less than the braincase width, whereas the length is three-quarters the width. In dorsal view, the posterior margin projects backwards; this projection and elongation of the braincase is most apparent in lateral view. The supraorbital rims are wide and flat without any indications of grooves for nasal glands. The width of the skull at the confluence of the frontals and ectethmoid plates is slightly greater than the width between the outer surfaces of the jugal bars; the dorsal end of the lateral nasal bars lies just medial to the edge of the skull. In lateral view, the anterior end of the supraorbital rim slopes down gradually to the base of the upper jaw. The orbit is a little lower and smaller than in *Pedionomus*, just under one-third the length of the skull, and the orbital septum is only partly ossified. A minute postorbital process is present on the lateral edge of the postorbital wall. The zygomatic process is well-developed and covers completely the dorsal head of the quadrate-squamosal articulation; this process is forked in *T. pyrrhothorax* and *varia*. The suprameatic process is fused with the zygomatic process, although the two processes are distinct in some (young?) specimens. No temporal fossa exists, although a shallow hollow is present on the lateral wall of the braincase just posterior to the edge of the orbit. A small suprameatic fossa is present on the ventrolateral surface of the zygomatic process. The lateral edge of the postorbital wall and the zygomatic process flare out to form a well-marked hollow on the lateral portion of the postorbital wall just dorsal to the quadrate. This hollow apparently serves as the origin of the M. adductor mandibulis externus rostralis. A small but distinct process lies at the anterodorsal edge of the auditory bulla just above the external auditory meatus in some species as *T. tanki, varia* and *pyrrhothorax*; this may be called the posterior meatic process.

The occipital plate is elevated about 30° above the axis of the basisphenoid rostrum. The base of the braincase is similar to that in *Pedionomus* except that the auditory bullae are rather flatter and the lateral processes of the basitemporal plate are slightly better developed.

ECTETHMOID: The ectethmoid plate is broader and merges fully and smoothly with the frontal; it forms a definite anterior wall of the orbit. It is thicker than in *Pedionomus* with the well-ossified alinasal filling the dorsal half of the antorbital cavity. The alinasal is fused rigidly with the ectethmoid and with the base of the upper jaw, extending as far forward as the ossified orbital septum with which it is continuous. In dorsal view, the ossified alinasal fills the posterior end of the nostril. The lacrymal appears to be absent. A small ectethmoid foramen (divided in *T. sylvatica*, U.S.N.M. 429078) is present at the mediodorsal corner of the ectethmoid plate and a minute foramen is present at or near the dorsolateral corner of the ectethmoid in a few forms (*T. varia*, A.M.N.H. 1601; and *T. suscitator*, U.S.N.M. 347288). The lateral foramen may be present in more specimens but could not be detected because of damage to the bone or because of dried tissue obscuring it. In some specimens a small groove is present at the junction of the ectethmoid plate and the supraorbital rims which probably corresponds to the

lateral foramen. A small foramen is present on the anterodorsal face of the ossified alinasal just anterior to the posterior end of the nostril; this foramen is the anterior opening of the canal starting at the medial ectethmoid foramen.

UPPER JAW: Except for the ossified alinasal, the upper jaw and nostril (schizorhinal) of *T. nigricollis* are similar to those of *Pedionomus*. The jaw of *T. pyrrhothorax* is shorter, stouter and less depressed than in *nigricollis* with heavier dorsal and ventral bars and a more massive anterior tip. The anterior extension of the ossified orbital septum, which has a lateral flange extending under the medial dorsal bar as in *Pedionomus*, is hidden by the alinasal in lateral view. The skull of *Turnix* is rhynchokinetic of the charadriiform type.

QUADRATE: The quadrate of *Turnix* is similar to that of *Pedionomus* with a few exceptions. The dorsal head of the squamosal articulation is completely hidden by the combined zygomatic and supermeatic processes. Both the lateral and the medial articular condyles are sharply defined knobs with a deep groove between them. The posterior condyle is reduced to a small, elevated knob immediately behind the medial condyle.

BONY PALATE: The pterygoid is slightly more massive and has a more distinct bend at the basipterygoid articulation than in *Pedionomus*. The mediopalatine processes meet along the midline. The palatine shelf is narrow with a gradually sloping posterolateral corner, (much squarer in some *T. pyrrhothorax* than as shown in Fig. 5C); the shelf is concave ventrally. A distinct interpalatine process and a long straight prepalatine process (= bar) are present.

The vomer comprises a pair of long thin processes extending from the palatine and a short pointed anteromedial plate. It is basically similar to the vomer in *Pedionomus* except that the anterior plate is shorter. The anterior plate of the vomer varies considerably among the species of *Turnix* (Fig. 7) from a plate of moderate width and pointed anterior tip to one of broad width and truncated tip with a pair of lateral horns. The anterior plate in *pyrrhothorax* is very broad and has a squared tip; the latter may be (but probably is not) the result of damage during preparation. Hence, the palate of *Turnix* varies from a fairly typical schizognathous one to an apparently aegithognathous one according to the criteria established in recent discussions (see below, p. 204–5); however, the palate of all species of *Turnix* is clearly schizognathous.

MAXILLO-PALATINES: The jugal bar, lateral nasal bar and base of the maxillopalatine pedicle meet at a common point, but the prepalatine bars arise from a more anterior point on the upper jaw. The pedicle of the maxillo-palatine is very thin and it usually meets and fuses to the prepalatine bar where it passes dorsally to that bone; the pedicle of the maxillo-palatine does not touch the prepalatine bar in *T. varia*. The free tip of the maxillo-palatine is a small plate that is scarcely larger than the width of the pedicle.

MANDIBLE: The mandible of most species of *Turnix* is slightly thinner and more decurved than that of *Pedionomus* (Figs. 4C, 5B, 8A, 9A and 9C). A small but distinct knob on the dorsal edge of the ramus may serve for the insertion of the M. adductor mandibulis externus rostralis; this knob correlates with the hollow on the lateral part of the postorbital wall. The articular surface is broad and flat except for a distinct groove for the medial condyle. A broad lateral shelf exists corresponding to the wide lateral condyle. The retroarticular process is long and narrow, and the internal process is long, narrow and curves forward at its tip. The posterior wall of the articular cavity is absent; hence, a deep groove separates the

retroarticular and internal processes. The tip of the internal process articulates with the ventral tip of the lateral process of the basitemporal plate (Fig. 8A).

The mandible of *T. pyrrhothorax* (Figs. 5B and 9C) is straight and deep with a moderately high coronoid process. A distinct bony knob is present at the postero-dorsal corner of the coronoid process, probably for insertion of the M. adductor mandibulis externus rostralis. The articular facet for the lateral condyle lies on the lateral flange and is considerably higher than the articular facet for the medial condyle. The retroarticular process is short, but the internal process is long, narrow and curves forward at its tip. The posterior wall of the articular cavity is absent. The massive mandible of this species corresponds to the heavy upper jaw.

ORTYXELOS

Although the skulls of the available specimens of *Ortyxelos* were badly damaged, most parts except the upper jaw could be examined and compared with Lowe's (1923) description and text. Basically the skull is very similar to that of *Turnix* as stated by Lowe. The major points of difference are as follow.

BRAINCASE: The postorbital process is completely lacking. The zygomatic process is smaller, but still covers the dorsal head of the quadrate-squamosal articulation. But the lateral edge of the postorbital wall forms a simple corner with the temporal wall of the braincase; the hollow seen in *Turnix* is absent.

ECTETHMOID: A small ectethmoid foramen is present at the mediodorsal corner of the ectethmoid and a second small foramen is present on the dorsal margin of the ectethmoid about halfway out to the lateral edge of the skull.

QUADRATE: The posterior articular condyle has disappeared completely, leaving the lateral and medial condyle as distinct knobs separated by a deep groove and lying in a straight line resulting in a quite unusual configuration; the structure of these condyles is not shown in Lowe's figure (1923, Fig. 2A).

PALATE: The two palatines apparently do not meet along the midline as shown by Lowe. The palatine is considerably smaller than in *Turnix* with a smaller and less concave palatine shelf, although the overall shape of the palatine in *Ortyxelos* is similar to that in *Turnix*.

The processes connecting the palatines with the anterior plate of the vomer are missing as noted by Lowe, although this may be due to incomplete ossification because of age. The vomer is moderately broad with a pointed tip and similar to that seen in some species of *Turnix* and in *Pedionomus*. We would characterize the palate of *Ortyxelos* as schizognathous.

MANDIBLE: The lower jaw of both specimens was lost. Lowe did not describe it.

COMPARISON

The skulls of *Turnix* and *Ortyxelos* are very similar as Lowe (1923) has noted previously. The absence of the posterior articular condyle of the quadrate in *Ortyxelos* is the culmination of a trend seen in *Turnix*. The lack of the postorbital process and of the hollow in the lateral edge of the postorbital wall in *Ortyxelos* versus the minute postorbital process and the distinct postorbital hollow in *Turnix*, and the differences in size of the palatines in the two genera are minor compared to the overall similarity of these genera and to the suite of differences between these genera and *Pedionomus*.

Although the skulls of *Pedionomus* and of *Turnix* appear to be basically similar, the degree of this resemblance and its interpretation cannot be ascertained

without further comparison with other birds. It is entirely possible that similarities between these genera indicate only that both forms are members of a broader group than an avian family. Hence, in this and all later comparisons, we shall emphasize only the differences between these genera, but with the warning that this method may introduce an artificial bias suggesting that these birds are more dissimilar and more distantly related than they actually are. No such conclusion is warranted on the factual basis of this study because of the lack of comparison with additional birds.

The braincase differs in its overall proportions, with *Pedionomus* having a higher, wider and shorter braincase with a larger orbit and narrow supraorbital rims. *Pedionomus* has a more distinct postorbital process, but lacks the large zygomatic process and has only a small hollow on the postorbital wall as opposed to the larger hollow in *Turnix*. The ectethmoid of the two genera is markedly different in size and shape, in the size of the ectethmoid foramen (large in *Pedionomus*) and in the presence of a large ossified alinasal fused to the anterior ectethmoid surface in *Turnix*. The articular condyles of the quadrate differ in that the posterior condyle is small and a distinct groove separates the lateral and medial condyles in *Turnix*. The size and shape of the palatines differ with this bone being smaller and having a sloping posterolateral corner in *Turnix*. The vomer of *Turnix* tends towards an aegithognathous condition in some species. The maxillo-palatines of *Turnix* are much narrower than those of *Pedionomus* with minutely expanded tips. The retroarticular and internal processes in *Turnix* are longer and narrow without a posterior wall connecting them. The lateral portion of the articular surfaces in *Turnix* flares out beyond the edge of the ramus.

Thus almost every portion of the skull of *Pedionomus* can be distinguished from those of *Turnix* with many of the differences being obvious and clear cut. *Ortyxelos* is close to *Turnix* and neither form can be regarded as a morphological intermediate between *Pedionomus* and the other genus.

STERNUM

PEDIONOMUS

The sternum of *Pedionomus* (Figs. 10 and 13A) is very broad in relation to its length; the width at the anterior end of the costal margin is just under one-half the length of the sternum. The sterno-coracoidal process is broad and short and flares out laterally in a low wide 'U' (Fig. 13A). The long coracoidal sulci are separated by a very short doubled dorsal manubrial spine; the ventral manubrial spine is lacking. The costal margin is long. The posterior lateral process is of medium length and width as the sternal notch extends about one-third the length of the sternum. The sternal plate and xiphial area are relatively wide. The anterior carinal margin is slightly concave, and the carinal apex is deep, just under one-half the length of the carina. The ventral margin of the carina slopes gradually upward toward the posterior tip of the sternum. The curvature in the carina (seen in ventral view) appears to be the result of preparation.

TURNIX

The sternum of *Turnix* (Figs. 11 and 13B) is quite narrow relative to its length; the width at the anterior end of the costal margin is just over one-fifth the length of the sternum. The sterno-coracoidal process is narrow and long and flares out laterally in a high, narrow 'U' (Fig. 13B). The short coracoidal sulci are separated by a long, narrow dorsal manubrial spine which has a very slight notch at its tip. A long lateral groove exists in the dorsal manubrial spine into which fits the

medial edge of the coracoid. The costal margin is very short and crowded onto the base of the sterno-coracoid process. The posterior lateral process is very long and narrow as the sternal notch extends well over one-half the length of the sternum. The posterior lateral process terminates in a distinct downward curving tip. The sternal plate and xiphial area are quite narrow. The carina is similar to that in *Pedionomus*, the curvature again resulting from preparation.

ORTYXELOS

With a few exceptions, the sternum of *Ortyxelos* (Figs. 12 and 13C) is similar to that of *Turnix*. The dorsal manubrial spine is short with a distinct groove at its tip; it lacks the lateral groove. The ventral manubrial spine is long and narrow. The posterior lateral process curves inward at its extremity and lacks a distinct tip. The tip of the xiphial area is expanded into a small knob.

Comparison

The main difference between *Ortyxelos* and *Turnix* is in the shape of the manubrium in which they are radically different. The sternum of *Pedionomus* is broader than that of *Turnix* with a shorter sternal notch and with a shorter sterno-coracoidal process and a shorter dorsal manubrial spine. The wider sternum in *Pedionomus* indicates larger flight muscles. The difference in the coracoidal sulcus and surrounding processes is reflected in the ventral end of the coracoid.

PECTORAL GIRDLE

PEDIONOMUS

Coracoid: The coracoid of *Pedionomus* (Fig. 14B) is slightly shorter than that of *Turnix*. Its ventral half is flat with elongated pointed processes flaring to each side. The sternal facet extends from the tip of the internal distal angle to the tip of the ventral process. The internal distal angle is the bluntest of the ventral processes and lies behind the dorsal manubrial spine. The sterno-coracoid process lies outside and covers most of the sterno-coracoid process of the sternum. The procoracoid is separated from the brachial tuberosity by a broad gap which forms the major part of the triosseal canal. The scapular facet is a distinct round hollow, whereas, the furcular facet is a flat indistinct area. The large glenoid facet lies just over the scapular facet.

Furcula: The two clavicles form a wide 'U'-shaped furcula (Fig. 15C) corresponding to the wide sternum. The furcular process is minute, almost non-existent. A long scapular tuberosity encloses the triosseal canal and attaches to a shallow groove on the medial surface of the scapula.

Scapula: The blade of the scapula (Fig. 16C) is long and slightly decurved toward a blunt apex. Its glenoid facet is small and lies just lateral to the coracoid articulation. A shallow groove on the medial anterior surface articulates with the clavicle. The acromion is a short, wide, blunt process.

TURNIX

Coracoid: The slightly longer and stouter coracoid of *Turnix* (Fig. 14C) has a curved ventral half with a long, deep concavity on its posterodorsal surface. The sternal facet is short and curved, with the internal distal angle lying in the lateral groove of the dorsal manubrial spine. The sterno-coracoid process is short, but still overlies the corresponding process on the sternum. The procoracoid is fused to

the brachial tuberosity (not complete in all specimens, e.g. *T. pyrrhothorax*) and, hence encloses the triosseal canal. A deep oblong scapular facet is present, but the furcular facet is flat and indistinct. The glenoid fossa lies just over the scapular facet.

FURCULA: The clavicles form a narrow 'U'-shaped furcula (Fig. 15B) corresponding to the narrow sternum. The furcular process is a flat, backwards-extending plate that almost reaches the carinal apex. No scapular tuberosity exists as the clavicle articulates only with the coracoid.

SCAPULA: The blade of the scapula (Fig. 16A) is long and decurves to a slightly expanded apex. The glenoid fossa is larger and lies lateral to the elongated slender acromion.

ORTYXELOS

CORACOID: The coracoid of *Ortyxelos* (Fig. 14A) is very similar to that of *Turnix* but the concavity on the posterodorsal surface is even deeper. A longer, truncated sterno-coracoid process appears to lie anterior to the corresponding process of the sternum. A gap separates the procoracoid and brachial tuberosity.

FURCULA: The furcula (Fig. 15A) is narrow with a flat furcular process similar to that in *Turnix*.

SCAPULA: The scapula (Fig. 16B) is similar in all respects to that of *Turnix*; the posterior end was damaged but appears to be somewhat expanded.

COMPARISON

Except for minor differences, the pectoral girdle of *Ortyxelos* is similar to that of *Turnix*. The entire ventral half of the coracoid in *Pedionomus* is radically different from that in *Turnix* corresponding to the difference in coracoidal sulcus. The deep posterior concavity in *Turnix* may also be related to the short coracoidal sulcus and a resulting curvature of the coracoid about its longitudinal axis. The long sulcus in *Pedionomus* may allow a flattened coracoid without a posterior concavity. However, the differences in the head of the coracoid are minor, limited mainly to the procoracoid brachial tuberosity connection. The wide furcula in *Pedionomus* as compared to the narrow furcula in *Turnix* reflects the difference in width of the sternum.

Basically, the entire suite of differences in the sternum and pectoral girdle of *Pedionomus* and *Turnix* are associated with a wide versus narrow sternum, and presumably, rib cage, in these two forms.

PECTORAL LIMB

PEDIONOMUS

HUMERUS: The humerus of *Pedionomus* (Fig. 17D) is long and slender, being one-third or more longer than the humerus of a *Turnix* of the same body size. Its head is a high dome with a distinct ligamental furrow running across its palmar surface. The external tuberosity is a slight shoulder on the humeral head just proximal to the low deltoid crest. The deltoid crest projects perpendicularly next to the shallow bicipital furrow, and lacks any overhang. The bicipital crest arises from the shaft in a gradual curve. Its pneumatic fossa is small and shallow and lacks a pneumatic foramen. The internal tuberosity is a distinct knob separated from the humeral head by a deep capital groove. The capital groove opens onto the anconal surface of the shaft and is separated from the pneumatic fossa by a well-developed medial crest of the pneumatic fossa. On the anconal surface, the external tuberosity

is a mere shoulder on the head with a faint pectoral attachment in its centre. The shaft is very slightly bowed. On the distal anconal surface, the tip of the ectepicondylar prominence may be just seen. The ectepicondyle and the inner condylar ridge are small, subequal, parallel ridges, separated by a shallow external tricipital groove. The external condyle cannot be seen in the anconal view. The olecranal fossa is broad and shallow, but distinct, with a shallow internal tricipital groove leading into it. The low internal trochlear condyle lies just distal to the olecranal fossa. The shaft curves out gently to the small rounded entepicondyle. The distal condyles lie on the same plane except for the internal condyle which projects slightly beyond the others. On the palmar surface the tip of the ectepicondylar prominence makes a sharp corner with the margin of the shaft; the prominence lies well above the large external trochlear condyle. This condyle lies at a 30° angle to the longitudinal axis of the shaft and its proximal end continues smoothly into the ectepicondyle. A wide, shallow intercondylar furrow separates the external and internal condyles. The rounded internal condyle and smaller entepicondyle project slightly beyond the external condyle. The small entepicondylar prominence is overshadowed by the more proximal attachment of the anterior articular ligament. The attachment of the pronator brevis is a minute projection on the internal margin of the shaft. A large, clear depression of the brachialis anticus lies on the internal half of the shaft.

Radius and Ulna: The radius and ulna of *Pedionomus* (Fig. 19B) are slightly longer than the humerus and are one-third to one-half longer than the corresponding bones in a *Turnix* of the same body size. The olecranon of the ulna is very small and short. The internal and external cotylae of the ulna lie on the same plane and face proximally. The shaft of the ulna curves slightly. The internal distal condyle is large, projects distally and has a slight medial depression; hence, it appears to have two parallel ridges. The external condyle is small and proximal to the internal distal condyle. Most of these condyles and their detailed structure cannot be seen on the figures.

Carpometacarpus: Only the metacarpals II and III of *Pedionomus* (Fig. 20A) are shown to illustrate the length of the carpometacarpus; again it is about one-half again the length of this bone in a *Turnix* of the same body size. The extensor process is high and does not slant proximally. Metacarpal III is straight and lies close to metacarpal II; hence, the intermetacarpal space is narrow.

TURNIX

Humerus: The humeri of several species of *Turnix* are shown in Figs. 17A, 17C and 18. *Turnix nigricollis* and *T. suscitator* are about the same body size as *Pedionomus*, whereas *T. varius* is about twice as large as *Pedionomus*. The humeral head is a lower, rounded dome with a very faint ligamental furrow on its palmar surface. The deltoid crest arises next to the faint bicipital furrow and has a sharp inward overhang. The bicipital crest curves sharply from the shaft and is much larger than in *Pedionomus*. Its entire anconal surface is occupied by an enormous pneumatic fossa that penetrates to the tip of the humeral head; however, no pneumatic foramen is present. The internal tuberosity lies perpendicular to the longitudinal axis of the bone across the proximal margin of the pneumatic fossa. The relatively shallow capital groove parallels the internal tuberosity and separates it from the humeral head. A distinct medial knob blocks the opening of the capital groove to the anconal surface. The external tuberosity is large with a huge groove for the pectoral attachment. The entire proximal head of the humerus curves intern-

ally much more than in *Pedionomus.* On the distal anconal surface, the tip of the large, pointed ectepicondylar prominence may be seen. The condyles are similar to those seen in *Pedionomus* but with the internal trochlear condyle and the entepicondyle projecting distally more and the entepicondyle flaring much more to the side. The olecranial fossa is very wide, but quite faint. On the palmar surface, the projecting ectepicondylar prominence lies well proximal to the condyles. The large external condyle appears to be double and extends proximally to the internal trochlear condyle; a narrow, deep intercondylar furrow separates the two condyles. The large rounded internal condyle and the entepicondyle lie on the same plane. A distinct attachment for the anterior articular ligament is present, and a clear impression for the brachialis anticus occurs in some forms (Figs. 17A).

Radius and Ulna: The radius and ulna of *Turnix* (Fig. 19A) are bowed much more than those of *Pedionomus.* The olecranon is large and projects proximally with the internal cotyla facing anteriorally. The external cotyla is wide and lies distal to the internal cotyla. The internal distal condyle is large and has a medial depression. The external condyle is small, elevated and separated from the internal condyle by a deep groove. Again, most of the details of these condyles cannot be seen on the figure.

Carpometacarpus: Only the metacarpals II and III of *Turnix* (Fig. 20B) are figured to show their relative shortness. The extensor process is low and projects proximally. Metacarpus III is bowed outward so that the intermetacarpal space is wide.

ORTYXELOS

Humerus: The humerus of *Ortyxelos* (Fig. 17B) is basically like that of *Turnix,* but with some clear differences. The humeral head is a high dome with a most indistinct ligamental furrow. The deltoid crest does not have a medial overhang. The bicipital crest curves out sharply from the shaft and has a large deep pneumatic fossa which does not penetrate into the humeral head as far as in *Turnix.* The internal tuberosity and deep capital groove are like those in *Turnix* with an abrupt medial knob blocking the opening of the capital groove onto the shaft. The distal condyles are very much as those in *Turnix,* except that the ectepicondylar prominence is a narrow projection from the shaft.

Radius and Ulna: The radius and ulna of *Ortyxelos* (Fig. 19C) are similar to those of *Turnix.* The external cotyla appears to be slightly smaller, however.

Comparison

The wing bones of *Ortyxelos* are similar to those of *Turnix* except for a few characteristics; namely, the absence of the medial overhang on the deltoid crest and the fact that the cavity of the pneumatic fossa stops short of the humeral head.

Pedionomus, on the other hand, differs considerably from *Turnix* in the structure of the wing skeleton. All of the bony elements in the wing of *Pedionomus* are one-third to one-half longer than the comparable elements in a *Turnix* of the same body-size, resulting in a wing that is remarkably long for a cursorial bird. The entire head of the humerus differs in the two birds, the important points being the smaller less flaring bicipital crest and small pneumatic fossa, lack of a medial overhang on the deltoid crest, deeper ligamental furrow on the palmar surface of the humeral head, smaller internal tuberosity, absence of a medial knob at the opening of the capital groove and smaller external tuberosity and pectoral attachment in *Pedionomus.* The differences in the distal end of the humerus are less marked and

are comprised mainly of the smaller ectepicondylar prominence, more distinct olecranial fossa, smaller and less projecting internal condyle and entepicondyle with the latter not flaring out from the shaft of the humerus, and a shallower wider intercondylar furrow in *Pedionomus*. The radius and ulna of *Pedionomus* are straighter with a smaller, shorter olecranon and smaller, coplanar internal and external cotylae with the latter not flaring as far from the shaft. The extensor process of the carpometacarpus in *Pedionomus* is higher and does not project proximally, and the metacarpal III is straight and lies close to the metacarpal II resulting in a narrow intermetacarpal space. The longer wings of *Pedionomus* may be correlated functionally with its broader sternum and presumably larger flight muscles.

SYNSACRUM

PEDIONOMUS

The synsacrum of *Pedionomus* (Fig. 21) is broad and flat. The foramina between the vertebrae may be simply the result of immaturity and incomplete ossification. The anterior blade of the ilium spreads out laterally in a flat curve. The posterior iliac plate is flat and terminates in a short posterior projection. The posterior iliac projection marks the termination of the iliac crest. When viewed from above or below, posteromedial margin of the synsacrum forms a wide shallow 'U'. The ischium extends posteriorly beyond the ilium and terminates in a narrow angle. The antitrochanter is small as is the pectineal process which is reduced to a mere corner at the anterior tip of the pubis. The pubis is narrow and flares widely to the side; in one specimen the posterior tip of the pubis curves slightly medially.

TURNIX

The synsacrum of *Turnix* (Fig. 22) is narrower and slightly deeper than that of *Pedionomus*. The anterior blade of the ilium drops vertically from the anterior iliac crest, and then spreads laterally; the anterior part flares out just before the anterior margin. The posterior iliac plate terminates in a minute process so that the posteromedial margin of the synsacrum is straight. A short, heavy process is present at the midpoint of the posterior iliac crest. The broad ischium extends posteriorly beyond the ilium and terminates in a broad, inward-curving angle. The pubis is broad and curves inward. The antitrochanter is large, and while the pectineal process is larger than in *Pedionomus*, it is still small.

ORTYXELOS

The synsacrum of *Ortyxelos* differs from that of *Turnix* only in that it lacks the heavy spine on the posterior iliac crest and the posterior iliac plate ends in a blunt projection.

Comparison

The major difference in the synsacrum of *Pedionomus* and *Turnix* is its greater width in *Pedionomus* with the posterior projections of the ischium and pubis flaring widely to the side. The ilium of *Pedionomus* has a prominent posterior projection that is absent in *Turnix*. The posterior iliac crest of *Pedionomus* is not as sharp and lacks the heavy process found in *Turnix*. The broad synsacrum of *Pedionomus* may be functionally or developmentally correlated with the broad sternum and pectoral girdle although the available evidence for such a correlation is meagre.

PELVIC LIMB

PEDIONOMUS

FEMUR: The head of the femur in *Pedionomus* (Fig. 23B) curves inwards from the shaft with a flat neck and iliac facet. The trochanter is well-developed and meets the iliac facet at a right angle. The obturator ridge is rather faint as is the trochanteric ridge. On the distal end of the bone, the internal condyle is flat and elevated above the external and fibular condyles; the intercondylar fossa is wide and shallow as is the popliteal area. The external and fibular condyles are subequal in size and are separated by a shallow fibular groove. On the anterior surface, the external and internal condyles are separated by a wide rotular groove. Considerable variation in length exists in the available specimens with the longest femur being 20% longer than the length of the shortest femur; the shortest femur is figured.

TIBIOTARSUS AND FIBULA: The tibiotarsus of *Pedionomus* (Fig. 24) is straight and over one-half again as long as the femur; that the fibula, in the present case, is quite short is considered to be the result of preparation since it extends about half-way down the tibio-tarsus in N.M.V. specimen No. B8872. The same variation in size exists in the tibiotarsus as in the femur; the shortest tibiotarsus is figured. The larger inner cnemial crest is a rounded plate, whereas the outer cnemial crest terminates in a distally projecting spine. The proximal articulating surfaces form a flat surface. As seen in posterior view, the internal and external distal condyles are subequal in size and separated by a broad intercondylar sulcus. The internal ligamental prominence curves smoothly from the shaft. On the anterior surface, the internal condyle projects anterior to the somewhat larger external condyle; the two condyles are separated by a broad anterior intercondylar fossa. In side view, the internal condyle has a distinct distal projection while the external condyle is almost circular. The supratendinal bridge is displaced toward the internal condyle. The tendinal groove is short and shallow.

TARSOMETATARSUS: The tarsometatarsus of *Pedionomus* (Fig. 26A) is the same length as the femur. The same range in size exists in the tarsometatarsus as in the femur and tibiotarsus; the middle-sized tarsometartarsus is figured. The proximal articulation is flat with the internal and external cotylae subequal in size and separated by a projecting intercotylar area. The hypotarsus comprises four tendinal canals and corresponding calcaneal ridges. Small inner and outer proximal foramina are present in a shallow anterior metatarsal groove; no posterior metatarsal groove exists. The distal foramen terminates a broad, shallow outer extensor groove. The trochlea for digit 2 is the most elevated one, is slightly posterior with a small wing and is separated from the trochlea for digit 3 by a wide internal intertrochlear notch. The trochlea for digit 3 projects the most distally and is the largest trochlea. The trochlea for digit 4 is elevated, but not as much as the trochlea for digit 2 and is separated from the trochlea for digit 3 by a narrow external intertrochlear notch. A very faint metatarsal facet exists on the ridge leading to the trochlea for digit 2 (not evident on the figure).

TURNIX

FEMUR: The femur of *Turnix* (Fig. 23A) is similar in size and structure to that of *Pedionomus*. It differs mainly in being straighter.

TIBIOTARSUS AND FIBULA: The tibiotarsus and fibula of *Turnix* (Fig. 25) are similar in size and most details of structure to those of *Pedionomus*. The distal projection on the internal condyle of *Turnix* is smaller than that of Pedionomus.

TARSOMETATARSUS: The tarsometatarsus of *Turnix* (Fig. 26B) is slightly shorter than that of *Pedionomus* but is similar in structure except for the lack of the metatarsal facet.

ORTYXELOS

The bones of the hind limb in *Ortyxelos* are very similar to those in *Turnix*.

COMPARISON

The hind limb is the most uniform part of the skeleton in *Pedionomus, Turnix* and *Ortyxelos,* the greatest difference being the presence of a hallux in *Pedionomus.*

Discussion

The description and comparison of the skeletons of *Pedionomus, Turnix* and *Ortyxelos* prompt some statements on the taxonomic relationships of these birds, and on some general problems such as the definition and recognition of palatal and nostril types. Each of these topics will be discussed in turn.

THE TURNICIDAE

On the basis of our comparisons of the skeletons of *Turnix* and of *Ortyxelos* with one another and more informally with members of the Charadriiformes, we concur completely with Lowe's (1923) conclusion that these birds are closely related. We share his surprise that *Ortyxelos* was separated from *Turnix* and placed in the Glareolidae, and would cite this earlier conclusion as an excellent example of the dangers in basing taxonomic decisions upon an inadequate study of characters.

All specimens of *Turnix* are quite uniform in the studied osteological features and differ from *Ortyxelos* in a few such as the complete absence in *Ortyxelos* of the posterior condyle of the quadrate, the lack in *Ortyxelos* of the bars connecting the vomer with the palatines, the radical difference in the shape of the manubrium of the sternum, and in a few aspects in the head of the humerus. These osteological differences in conjunction with plumage differences are sufficient to warrant the accepted generic distinction between these taxa. But, no matter what final decision is reached concerning the taxonomic distinction between *Turnix* and *Pedionomus, Ortyxelos* must remain in the same family-level taxon containing *Turnix*. Even if *Pedionomus* proves to be widely separated from *Turnix*, no justification exists for separating *Ortyxelos* and *Turnix* as distinct subfamilies.

TURNIX AND *PEDIONOMUS*

Interpretation of the comparisons of the skeletons of *Pedionomus* and *Turnix* (and *Ortyxelos*; in the following discussion, we include *Ortyxelos* under the term *Turnix*) is far more difficult. It is certainly not valid to regard *Pedionomus* simply as a slightly differently plumaged *Turnix* with a hallux. The osteological differences between these genera include many features of the skull and lower jaw, sternum and pectoral girdle, wing and synsacrum. Only in the elements of the leg are these genera similar to one another. These genera can be distinguished and recognized from one another with greater ease than can many families of non-passerine birds. One may argue with ease that differences are far easier to recognize between small taxa than between taxa with many members. And the observed differences must be analyzed functionally and taxonomically, neither of which can be done properly at this time.

So little is known about the habits of *Pedionomus* at this time that the functional

significances of the observed morphological differences could only be guessed, and with rather wild guesses. We propose only to point out some of the possible functional units and group the different features into these larger complexes. The set of differences in the skull and mandible would constitute at least one major functional complex distinct from all other complexes of the skeleton. However, it is not possible to distinguish between functional units within the skull at this time, although some of the differences do not appear to be closely related functionally. The whole set of differences in the sternum, pectoral girdle and possibly even the synsacrum may all be closely related and may be associated with a general broadening of the entire body skeleton of *Pedionomus* relative to the narrow skeleton of *Turnix*. (Or the body skeleton of *Turnix* may have become narrower.) These features are almost certainly not all correlated functionally, but may be parts of a large developmental complex involving the entire trunk skeleton. The details of the argument supporting this suggestion will be outlined step by step.

The elongated wing bones in *Pedionomus* and the suite of differences in the humerus would constitute a functional complex; the function and the adaptive significance of longer wings in *Pedionomus* are obscure at best. The longer wings may require stronger flight muscles which would influence the configuration of the sternum and pectoral girdle. Thus the complex of wing bones may be closely related with the elements of the sternum and pectoral girdle, and indeed the wing, pectoral girdle and sternum may constitute a single large functional complex. The selection forces acting upon the different characteristics of flight in *Turnix* and *Pedionomus* would act upon this entire complex. These selection forces would favour the longer wings in *Pedionomus*, the required larger flight muscles and hence the broadened sternum and pectoral girdle. As mentioned above, many of the detailed differences in the pectoral girdle and sternum appear to be associated with a general broadening of this part of the skeleton. Broadening of the pectoral girdle and sternum may have occurred by selection favouring a general broadening of the growth field controlling this part of the skeleton. Or, quite possibly, broadening of the anterior half of the trunk skeleton may have occurred by modification of a growth field that controlled the width of the entire trunk skeleton. Hence selection for a different flight pattern requiring larger flight muscles in *Pedionomus* would result in a broader synsacrum simply because this element is part of the trunk skeleton under the control of the broadening growth field being favoured by selection. This line of argument follows that proposed by Davis (1964, 1966) in his explanation of growth-related features in which an adaptive modification in one feature resulted in changes in many other features for which no functional and adaptive explanation could be offered.

It is possible that the whole suite of skeletal differences between *Pedionomus* and *Turnix* may be reduced to major differences in the set of features comprising the cranial functional unit and in the set of bony elements comprising the flight functional unit and the trunk developmental complex. We do not condense the many differences between *Turnix* and *Pedionomus* as a means of underestimating the dissimilarites between these taxa, but present this discussion to prevent a simple tabulation of all the described differences between these genera. Such a tabulation would result in redundant listing of the same difference under different features and in a great overestimation of the distinction between these genera. In conclusion we would like to emphasize that if the total differences between *Pedionomus* and *Turnix* prove to be modifications in the two functional units of the cranium and the flight apparatus, these modifications would be major ones that cannot be treated casually.

The taxonomic implications of these osteological comparisons of *Turnix* and of *Pedionomus* are equally difficult to assess because of our limited comparative base. These genera share many points of similarity and are probably members of a monophyletic taxon but the taxonomic rank of this taxon and whether any other genera or families of birds should be included are still open to question. It does seem reasonable to retain the generally accepted suborder Turnices within the Gruiformes for *Turnix, Ortyxelos* and *Pedionomus*. Yet we have little evidence from our study to support the inclusion of the Turniees in the Gruiformes. Within the Turnices, *Turnix* and *Pedionomus* have been distinguished on the familial and subfamilial levels. Interpretation of our evidence could support either position as well as considering these genera as members of distinct superfamilies. If all the differences are tabulated, the list becomes quite impressive and would support a conclusion that *Pedionomus* and *Turnix* belong to different superfamilies, or may not even be related at all but have converged toward each other in size and habits. We should point out that earlier systematists have allied *Turnix* with the galliform birds, perhaps being misled by the convergent similarity between *Turnix* and *Coturnix* of the Phasianidae. And *Ortyxelos* had been separated from *Turnix* and placed in a family belonging to a different order. At the other extreme, one could argue that many of the differences between *Turnix* and *Pedionomus* are all associated with modifications in either the cranium or the flight apparatus, the actual difference between the two genera being far less than the impressive list of individual differences. We are not prepared to defend either position at this time, nor do we wish to accept the easy compromise position. We do wish to emphasize that it is misleading to characterize *Pedionomus* as a *Turnix* with a hind toe. These genera are far more distinct, but may still prove to be members of the same family.

As a practical taxonomic solution, we would support the generally accepted position of placing *Turnix* and *Ortyxelos* in the Turnicidae and *Pedionomus* in the Pedionomidae, both families being included in the Turnices.

These equivocal taxonomic conclusions are far less than satisfactory but little more can be expected in the light of our very restrictive comparative base. Yet on the positive side are the facts that the comparisons do indicate strongly that *Turnix* and *Pedionomus* are more closely related to one another than to other gruiform birds, and that considerably more information is available with which to compare *Pedionomus* with other birds.

Pneumaticy

A minor but interesting feature of the skeleton of these genera is that it appears to be completely non-pneumatic in that no foramen for air sacs could be found. For example, no pneumatic foramen is present in the humerus in spite of the extremely deep pneumatic fossa in *Turnix* and *Ortyxelos*.

Palatal Types

The variation in the shape of the vomer in *Turnix* has an important bearing upon the concept of palatal types in birds and recent treatment (uses and abuses) of them. In Huxley's (1867) original description of palatal types in birds, he included the entire palate in his definition of each type. Shortly thereafter, attention was focused upon the condition of the vomer and maxillopalatines which became the important and usually sole criterion for each palate type. Hence, the major hallmark for the aegithognathous palate is a broad vomer with a truncated anterior margin, whereas for the schizognathous palate it is the narrow vomer with a sharp pointed anterior tip. These simplified criteria omit many of the basie

aspects of the palatal types used by Huxley. More significantly, they permit erroneous recognition of palates corresponding to each type and lead to serious misconceptions of the possible affinities of some birds and of the value of palatal types in classification of birds. On the basis of the shape of the vomer, the several species of *Turnix* (Fig. 7) range from a fairly typical schizognathous form to a fairly typical aegithognathous form. But if all the criteria cited by Huxley (1867: 426, 450-451) are used, the palates of *Turnix* as well as *Ortyxelos* and *Pedionomus* are clearly schizognathous. The broadening of the vomer and truncation of its anterior tip in some forms are part of a graded series of modifications in *Turnix* resulting in a broad truncated vomer in a few species. But this change is not toward the condition of the aegithognathous palate except in the shape of the vomer. Broadening the vomer could be associated simply with greater width of the skull or with increased need for support of the floor of the nasal cavity, and could have occurred independently several times among schizognathous birds.

Hence in spite of the broad, truncated vomer in several species of *Turnix*, we regard the palate of all members of the Turnices as schizognathous. We urge that Huxley's original criteria for palate types be followed carefully and that complete descriptions be given of any palates that may be mis-identified as the wrong type if the condition of the vomer and maxillopalatines are used as the only criteria.

Nostril Types

The nature of the nostrils in the Turnices posed a problem similar to that of the palate, namely they do not correspond exactly to the original descriptions. The original definition (Garrod 1873; and see Appendix 2) of the holorhinal versus the schizorhinal nostril is based upon the shape of the posterior end of the nostril (rounded versus a narrow slit) and the position of the posterior end of the nostril relative to the nasal-frontal hinge at the base of the upper jaw (anterior to the hinge versus posterior to the hinge). Hence, the original definition of the schizorhinal nostril indicates one possessing a narrow, slit-like posterior end that projects posteriorly beyond the nasal-frontal hinge. The slit-like posterior end became the criterion for the schizorhinal nostril while the rounded posterior end was used as the criterion for the holorhinal nostril.

The important functional differences between the holorhinal and schizorhinal nostrils are reflected in whether or not the nostril projects back beyond the nasal-frontal (kinetic) hinge of the upper jaw. The holorhinal nostril falls short of the nasal-frontal hinge and does not separate the hinge line of the lateral nasal bars from that of the medial dorsal bar (Bock 1964a). It is associated functionally with the prokinetic type of kinesis and with the ratite type of rhynchokinesis. The schizorhinal nostril projects back beyond the nasal-frontal hinge and separates the hinge line of the lateral nasal bars from that of the medial dorsal bar. It is associated functionally with the charadriiform type of rhynchokinesis. Whether the posterior end of the nostril is rounded or pointed does not influence in the least this functional consequence of the two nostril types. And the shape of the posterior end of the nostril does not have any independent functional significances.

Hence, the least important one of the two original criteria of the nostril types was chosen as the major and often sole criterion. We would recommend strongly that the distinction between the holorhinal and the schizorhinal nostril be based upon whether the posterior end of the nostril stops anterior to, or projects behind, the nasal-frontal hinge (i.e., separates the hinge of the medial dorsal bar from the hinge of the lateral nasal bars). The nostril of the Turnices is clearly schizorhinal because it projects well behind the nasal-frontal hinge in spite of the fact that its

posterior end is rounded. The broad nostril with a rounded posterior end in these birds is correlated with the broadening of the anterior part of the skull, as in the Glareolidae (Bock 1964b). To designate the nostril of these birds as holorhinal or pseudoholorhinal because the posterior end of the nostril is rounded obscures the most important morphological and functional property of the nostril in these birds. The term pseudoholorhinal is best dropped from usage, or restricted strictly to those birds that possess a prokinetic skull as adults and a slit-like holorhinal nostril with indications that this prokinetic condition has evolved secondarily from a rhynchokinetic skull and the original schizorhinal nostril has been modified toward a holorhinal condition.

Summary

1. The skeleton of *Pedionomus* is described and compared with those of *Turnix* and *Ortyxelos*. *Turnix* and *Ortyxelos* are quite similar to one another in most features of their skeleton, but are quite different from *Pedionomus* in many characteristics of the skull, sternum, pectoral girdle, wing and synsacrum. Only the elements of the hind limb are similar in these genera. The cranial differences include a smaller ectethmoid, lack of an ossified alinasal, more robust palatines, larger maxillo-palatines, larger postorbital process and smaller zygomatic process in *Pedionomus*. The sternum, pectoral girdle and synsacrum of *Pedionomus* are considerably wider than the corresponding elements in *Turnix* with numerous differences in detail. All elements of the wing of *Pedionomus* are longer than those of *Turnix* with some striking differences in the head of the humerus.

2. The osteological evidence supports the current taxonomic status of *Turnix* and *Ortyxelos* as separate genera in the family of Turnicidae. *Pedionomus* is more distinct from these birds—it is not simply a *Turnix* with a hallux—but it is not possible to decide at this time the level of taxonomic distinctiveness of these birds. As a practical taxonomic conclusion, it is suggested that the general practice of placing *Pedionomus* in a separate family, the Pedionomidae, be maintained.

3. Several confusing points in the definitions of the schizognathous and aegithognathous palates and of the holorhinal and schizorhinal nostrils are discussed. It is concluded that the members of the Turnices possess a schizognathous palate and a schizorhinal nostril.

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Appendix 1

This paper provides a good opportunity to correct a series of inexcusable errors made by Bock concerning the names applied to the basipterygoid articulation and the basitemporal articulation which were brought to his attention several years ago by McEvey.

The basipterygoid articulation is between the pterygoid bone and the basipterygoid process on the basisphenoid rostrum. It is found in many groups of tetrapods and is sometimes called the basal articulation. In two earlier papers (Bock 1959, 1960) this articulation was called the basisphenoid articulation, a poor name but not entirely wrong. However, in later papers (Bock 1963, 1964b) this articulation was called the basitemporal articulation, the basipterygoid process called the basitemporal process and the basisphenoid rostrum called the basitemporal rostrum. These terms are absolutely wrong and probably arose because of a confusion between the several 'basi-' terms. In Bock (1964a: 5-6) and the present paper, the correct terms of basipterygoid process and basipterygoid articulation are used and should be followed.

The basitemporal articulation (or articular-basitemporal articulation) is between the internal (= medial) process of the mandible and some process on the basitemporal plate (Bock 1960); it is also called the secondary articulation of the mandible. The brace formed by these bones abutting against one another has been called the medial brace of the mandible (Bock 1959, 1960). In Bock (1964a: 9, 1964b: 393) and in the present paper this articulation is called the basitemporal articulation and/or the secondary articulation of the mandible; either term is acceptable, but the term basitemporal articulation can be used only for this structure.

Appendix 2

After the manuscript was completed, we checked the literature for the reference of the original description for the terms holorhinal and schizorhinal; these were proposed by Garrod (1873). Much to our surprise, we discovered that Garrod figured the skull of *Pedionomus torquatus* as one of his original examples of a schizorhinal bird (Fig. 7, p. 34), although he did not include this genus in his list of schizorhinal birds (pp. 36-37). Hence our statement that Gadow's study (1891) is the only anatomical study of this bird is in error. Gadow (1891) had also overlooked this figure for he states that no earlier anatomical work on *Pedionomus*

exists and notes (p. 206), 'Garrod does not mention it at all'. The specimen figured by Garrod is probably lost as we were unable to locate any skeletal material in British museums, nor did Gadow indicate the existence of any specimens other than the two sent to the Cambridge Museum of Zoology from Australia shortly before he undertook his study.

It may be noted that Garrod included the Turnicidae (presumably including *Pedionomus*), the Glareolidae, the Pteroclidae and the Columbae among his list of schizorhinal birds. He does not say whether he had been able to examine skulls of the Thinocoridae although he does include the Limicolae (excluding the Burhinidae) among the schizorhinal birds. Many of these birds are considered to be holorhinal by recent workers although we concur with Garrod's original interpretations.

Abbreviations Used in the Figures

Skull

ab = auditory bulla
an = alinasal
ba = basipterygoid articulation
bsr = basisphenoid rostrum
bta = basitemporal articulation
btp = basitemporal plate
cpm = coronoid process of mandible
ect = ectethmoid plate
ectf = ectethmoid foramen
epm = external process of mandible
et = eustachian tube
fm = foramen magnum
ipm = internal process of mandible
ipp = interpalatine process
j = jugal bar
lbtp = lateral basitemporal process
lc = lateral condyle of quadrate
lnb = lateral nasal bar
lqf = lateral quadrate facet
mc = medial condyle of quadrate
mf = mandibular fossa
mp = maxillopalatine
mpp = mediopalatine process
mqf = medial quadrate facet
n = nostril
obp = orbital process of quadrate
ocp = occipital plate
os = orbital septum
otp = otic process of quadrate
p = palatine
pc = posterior condyle of quadrate
pmp = posterior meatic process
pp = postorbital process
ppb = prepalatine bar
ps = palatine shelf
pt = pterygoid
q = quadrate
rpm = retroarticular process of mandible
smf = suprameatic fossa
smp = suprameatic process
sr = supraorbital rims
tf = temporal fossa
v = vomer
zp = zygomatic process

Sternum and Pectoral Girdle

acm = anterior carinal margin
acr = acromion
bt = brachial tuberosity
c = carina
cm = costal margin
cs = coracoidal sulcus
dms = dorsal manubrial spine
ff = furcular facet
fp = furcular process
gf = glenoid facet
ida = internal distal angle
pcc = posterior coracoidal concavity
plp = posterior lateral process
proc = procoracoid
scf = scapular facet
scp = sternocoracoidal process
scpc = sternocoracoidal process of coracoid
sf = sternal facet
sn = sternal notch
sp = sternal plate
st = scapular tuberosity
tc = triosseal canal
vms = ventral manubrial process
vp = ventral process
xa = xiphial area

Pectoral Limb

aal = attachment of anterior articular ligament
apb = attachment of the pronator brevis
bc = bicipital crest
bf = bicipital furrow
cg = capital groove
dba = depression brachialis anticus
dc = deltoid crest
ecc = ectepicondyle
ecp = ectepicondylar prominence
enc = entepicondyle
et = external tuberosity
etc = external trochlear condyle
etg = external tricipital groove
expm = extensor process of metacarpus
h = head of humerus
icf = intercondylar furrow
icr = inner condylar ridge

idc = internal distal condyle
ims = intermetacarpal space
it = internal tuberosity
itc = internal trochlear condyle
itg = internal tricipital groove
lf = ligamental furrow
m II = metacarpal II
m III = metacarpal III
mcp = medial crest of pneumatic fossa
mk = medial knob of humerus
of = olecranal fossa
ol = olecranon
pa = pectoral attachment
pf = pneumatic fossa
r = radius
u = ulna

Synsacrum

abil = anterior blade of ilium
ac = acetabulum
ant = antitrochanter
il = ilium
ilc = iliac crest
is = ischium
isa = ischial angle
pep = pectineal process
pilc = process of iliac crest
ppil = posterior projection of ilium
pu = pubis

Pelvic Limb

aif = anterior intercondylar fossa
amg = anterior metatarsal groove
dmf = distal metatarsal foramen
ec = external condyle of femur
edct = external distal condyle of tibiotarsus
etn = external intertrochlear notch
fcf = fibular condyle of femur
fib = fibula
fig = fibular groove
hcr = hypotarsal calcaneal ridge
hf = head of femur
htc = hypotarsal tendinal canal
hyp = hypotarsus
icc = inner cnemial crest
icf = internal condyle of femur
ics = intercondylar sulcus
idct = internal distal condyle of tibiotarsus
ilf = iliac facet
ilp = internal ligamental prominence
inf = intercondylar fossa
itn = internal intertrochlear notch
mtf = metatarsal facet
nf = neck of femur
obr = obturator ridge
occ = outer cnemial crest
oeg = outer extensor groove
pa = popliteal area
peco = proximal external cotyla
pico = proximal internal cotyla
pmf = proximal metatarsal foramen
rg = rotular groove
stb = supratendinal bridge
td 2 = trochlea for digit 2
td 3 = trochlea for digit 3
td 4 = trochlea for digit 4
tng = tendinal groove
trf = trochanter of femur
trr = trochanter ridge
tt = tibiotarsus

Explanation of Text-Figures 1-26

FIG. 1—The skull and mandible of *Pedionomus torquatus*. The skull (N.M.V. W6698) is shown in dorsal view (A), lateral view (B) and ventral view (D), and the mandible is shown in lateral view (C). An isolated vomer (N.M.V. W6084) is shown in ventral view (E) at the same approximate size and anteroposterior position relative to the ventral view of the skull. The vomer may be slightly larger than correct relative size. The key to the abbreviations used in this and other figures will be found on pp. 209-210. Approximately 3½ times life size.

FIG. 2—The squamosal region of the skull of *Pedionomus torquatus* (N.M.V. W6084) to show the details of the articular facets for the quadrate and processes adjacent to the lateral quadrate facet. Approximately 17 times life size.

FIG. 3—The isolated vomer of *Pedionomus torquatus* (N.M.V. W6084) seen in ventral view (A) and dorsal view (B). The long articular grooves on the dorsal side of the posterior processes and their correspondence to the elongated anterior processes from the palatines (Fig. 1D) should be noted. Approximately 17 times life size.

FIG. 4—The skull and mandible of *Turnix nigricollis* (A.M.N.H. 5381). The skull is shown in dorsal view (A), lateral view (B) and ventral view (D), and the mandible is shown in lateral view (C). Approximately 4 times life size.

FIG. 5—The skull and mandible of *Turnix pyrrhothorax* (N.M.V. 665), the heaviest-billed species in the genus. Tbe skull is shown in lateral view A) and ventral view (C), and the mandible is shown in lateral view (B). Note the depth of the mandibular ramus and the well developed coronoid process. Approximately 4 times life size.

FIG. 6—The skull of *Turnix varia* (A.M.N.H. 1601), one of the largest species in the genus, shown in lateral view. Approximately 3½ times life size.

FIG. 7—The vomer of several species of *Turnix*, seen in ventral view, to show the great range of variation and trend toward an aegithognathous-like vomer in the extreme case. The species shown are: (A) *T. sylvatica* (U.S.N.M. 429078); (B) *T. nigricollis* (A.M.N.H. 5381); (C) *T. tanki* (A.M.N.H. 1581); (D) *T. nigricollis* (A.M.N.H. 1994); (E) *T. sylvatica* (U.S.N.M. 344362); (F) *T. sylvatica* (U.S.N.M. 344365); (G) *T. varia* (A.M.N.H. 1601); and (H) *T. pyrrhothorax* (N.M.V. 665). Approximately 16 times life size.

FIG. 8—The cranial base and mandible of (A) *Turnix nigricollis* (A.M.N.H. 5381) and (B) *Pedionomus torquatus* (N.M.V. W6698) seen in ventral view. The mandible has been replaced upon its quadrate articulation so that its relationships to other parts of the skull may not be exactly correct. Note the basitemporal articulation between the internal process of the mandible and the lateral process of the basitemporal plate and the basipterygoid articulation between the pterygoid and the basipterygoid process of the braincase (see the discussion in Appendix 1). Approximately 7 times life size.

FIG. 9—The mandible of (A) *Turnix nigricollis* (A.M.N.H. 5381), (B) *Pedionomus torquatus* (N.M.V. W6698), and (C) *Turnix pyrrhothorax* (N.M.V. 665) seen in dorsal view to show the details of the articular surfaces. Approximately 6½ times life size.

FIG. 10—The sternum of *Pedionomus torquatus* (N.M.V. W6084) seen in dorsal view (A), lateral view (B), and ventral view (C). Approximately 3 times life size.

FIG. 11—The sternum of *Turnix nigricollis* (A.M.N.H. 5381) seen in dorsal view (A), lateral view (B), and ventral view (C). Approximately 3¾ times life size.

FIG. 12—The sternum of *Ortyxelos meiffrenii* (B.M.N.H. S/1952.2.71) seen in dorsal view (A), lateral view (B), and ventral view (C). Approximately 5 times life size.

FIG. 13—The sternum of (A) *Pedionomus torquatus* (N.M.V. W6084), (B) *Turnix nigricollis* (A.M.N.H. 5381), and (C) *Ortyxelos meiffrenii* (B.M.N.H. S/1952.2.71) seen in anterior view. Approximately 3½ times life size.

FIG. 14—The coracoid of (A) *Ortyxelos meiffrenii* (B.M.N.H. S/1952.2.71), (B) *Pedionomus torquatus* (N.M.V. W6084), and (C) *Turnix nigricollis* (A.M.N.H. 5381) seen in posterodorsal view (left figure) and anteroventral view (right figure). Approximately 3½ times life size.

FIG. 15—The furcula of (A) *Ortyxelos meiffrenii* (B.M.N.H. S/1956.2.1), (B) *Turnix nigricollis* (A.M.N.H. 5381), and (C) *Pedionomus torquatus* (N.M.V. W6698) seen in lateral view (left figure) and anterior view (right figure). Approximately 3 times life size.

FIG. 16—The scapula of (A) *Turnix nigricollis* (A.M.N.H. 5381), (B) *Ortyxelos meiffrenii* (B.M.N.H. S/1952.2.71), and (C) *Pedionomus torquatus* (N.M.V. W6698) seen in lateral view. Approximately 4½ times life size.

FIG. 17—The humerus of (A) *Turnix nigricollis* (A.M.N.H. 5381), (B) *Ortyxelos meiffrenii* (B.M.N.H. S/1956.22.1), (C) *Turnix suscitator* (U.S.N.M. 347288), and (D) *Pedionomus torquatus* (N.M.V. W6698) seen in anconal view (left figure) and palmar view (right figure). Approximately 3½ times life size.

FIG. 18—The humerus of *Turnix varia* (A.M.N.H. 1601) seen in anconal view (top figure) and palmar view (bottom figure). Approximately 3½ times life size.

FIG. 19—The radius and ulna of (A) *Turnix nigricollis* (A.M.N.H. 5381), (B) *Pedionomus torquatus* (N.M.V. W6655), and (C) *Ortyxelos meiffrenii* (B.M.N.H. S/1952. 2.71) seen in ventral view. Approximately 3½ times life size.

FIG. 20— The carpometacarpus of (A) *Pedionomus torquatus* (N.M.V. W6084), and (B) *Turnix nigricollis* (A.M.N.H. 5381) to show the relative lengths of the main element. In *Pedionomus*, the left figure is the dorsal view and the right figure the ventral view. In *Turnix*, the left figure is the ventral view and the right figure the dorsal view. Approximately 4½ times life size.

FIG. 21—The synsacrum of *Pedionomus torquatus* (N.M.V. W6655) seen in dorsal view (A), lateral view (B), and ventral view (C). The ends of the pubis have been cut off to fit the drawings into one figure. Approximately 3 times life size.

FIG. 22—The synsacrum of *Turnix nigricollis* (A.M.N.H. 5381) seen in dorsal view (A), lateral view (B), and ventral view (C). Approximately 3½ times life size.

FIG. 23—The femur of (A) *Turnix nigricollis* (A.M.N.H. 5381), and (B) *Pedionomus torquatus* (N.M.V. W6698) seen in posterior view (left figure) and anterior view (right figure). Approximately 4 times life size.

FIG. 24—The tibiotarsus and fibula of *Pedionomus torquatus* (N.M.V. W6698) seen in (A) anterolateral, (B) posteromedial, (C) posterior, and (D) anterior views. Approximately 3½ times life size.

FIG. 25—The tibiotarsus and fibula of *Turnix nigricollis* (A.M.N.H. 5381) seen in (A) anterolateral, (B) posteromedial, (C) posterior and (D) anterior views. Approximately 3½ times life size.

FIG. 26—The tarsometatarsus of (A) *Pedionomus torquatus* (N.M.V. W6655), and (B) *Turnix nigricollis* (A.M.N.H. 5381) seen in anterior view (left figure) and posterior view (right figure). Approximately 5 times life size.

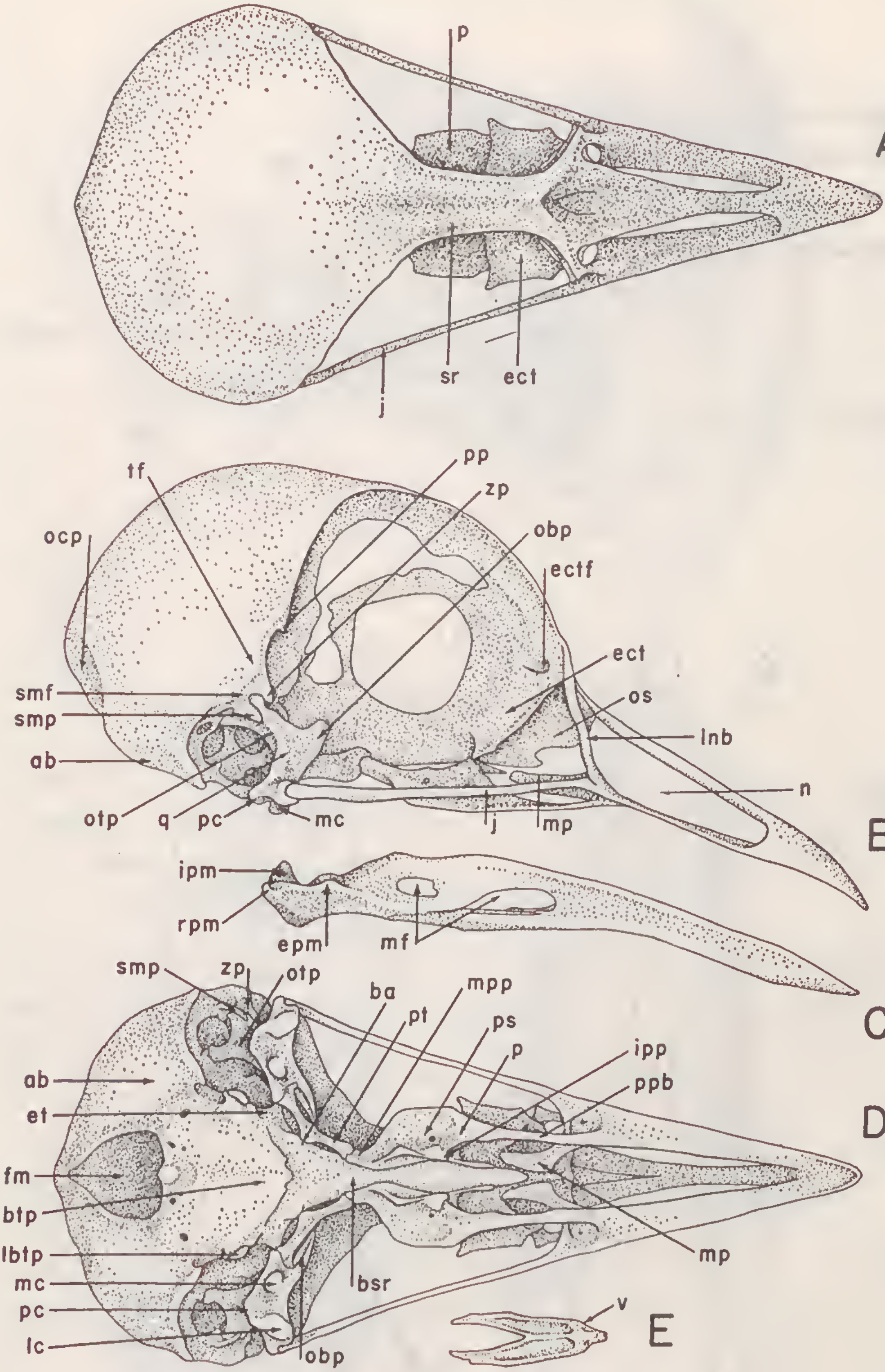

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Fig. 1

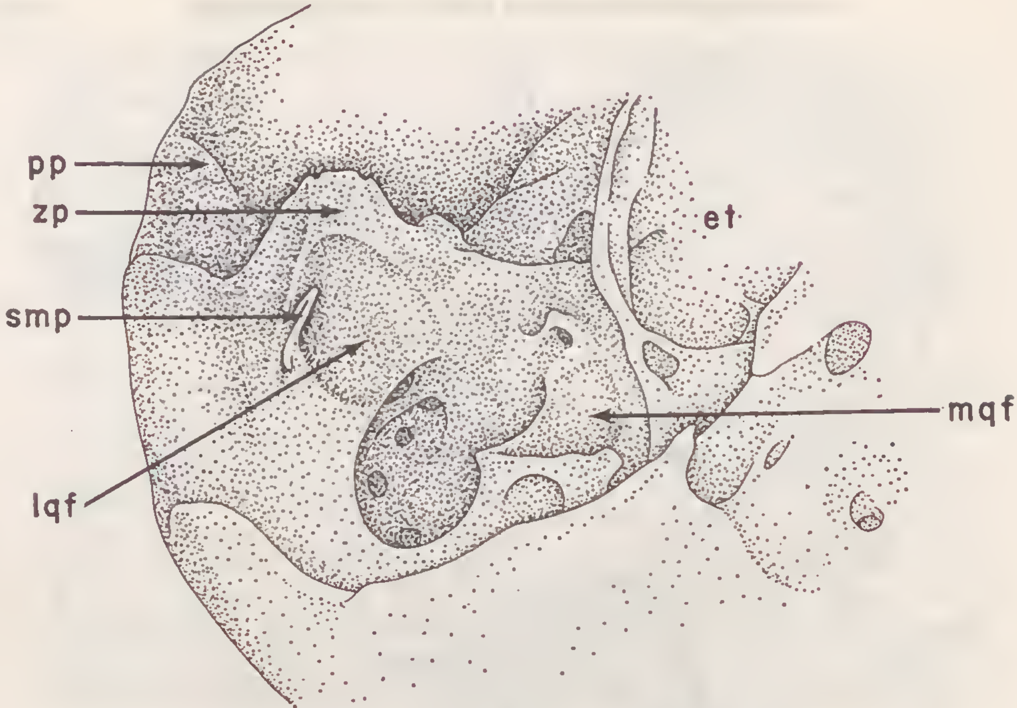
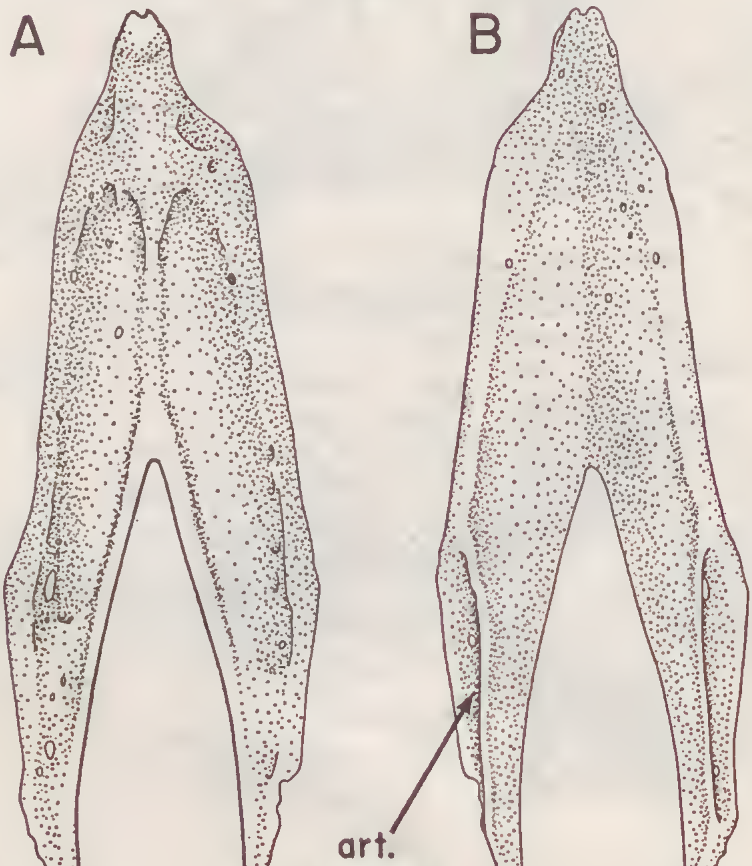


Fig. 2



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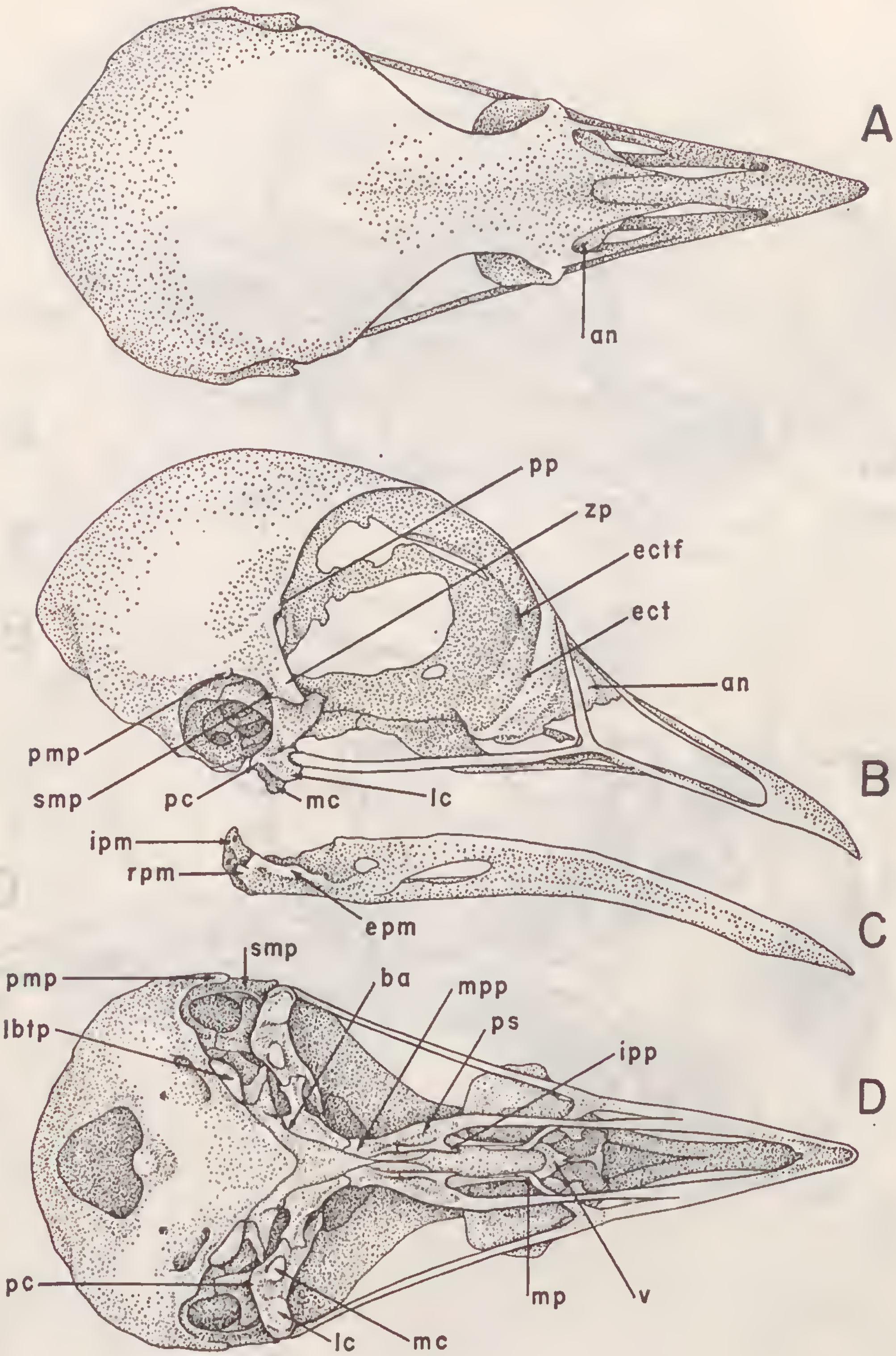
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Fig. 4

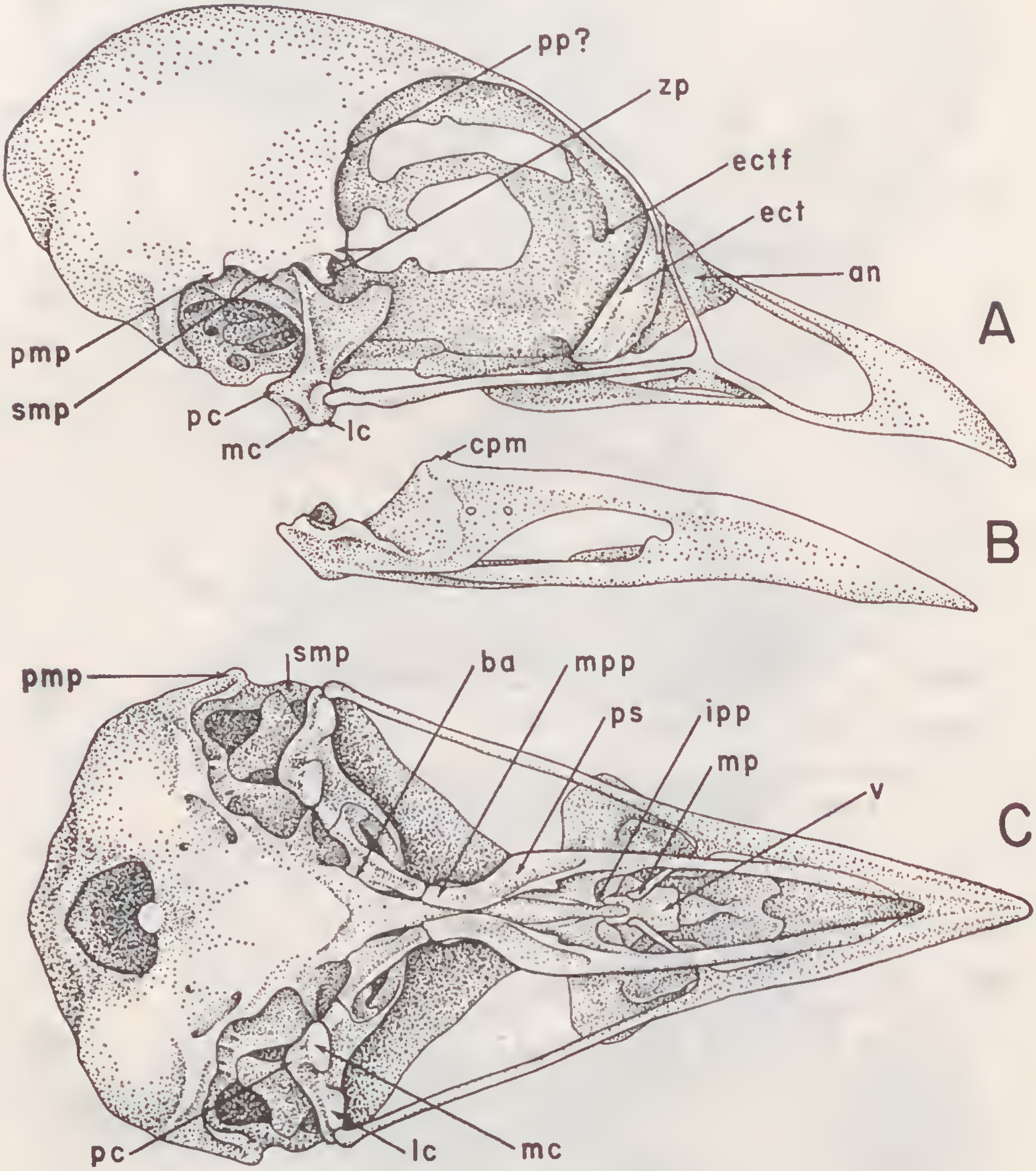
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Fig. 5

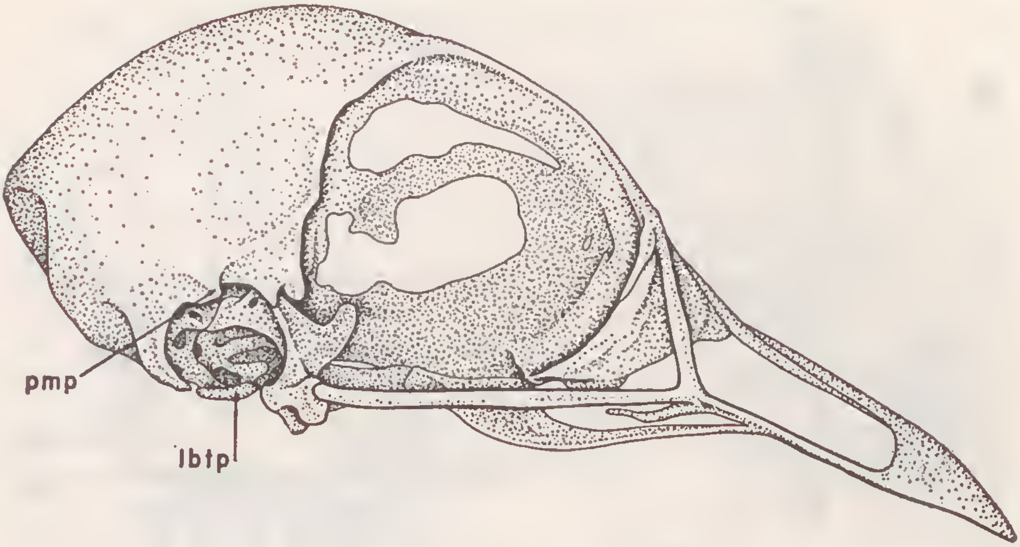

Fig. 6

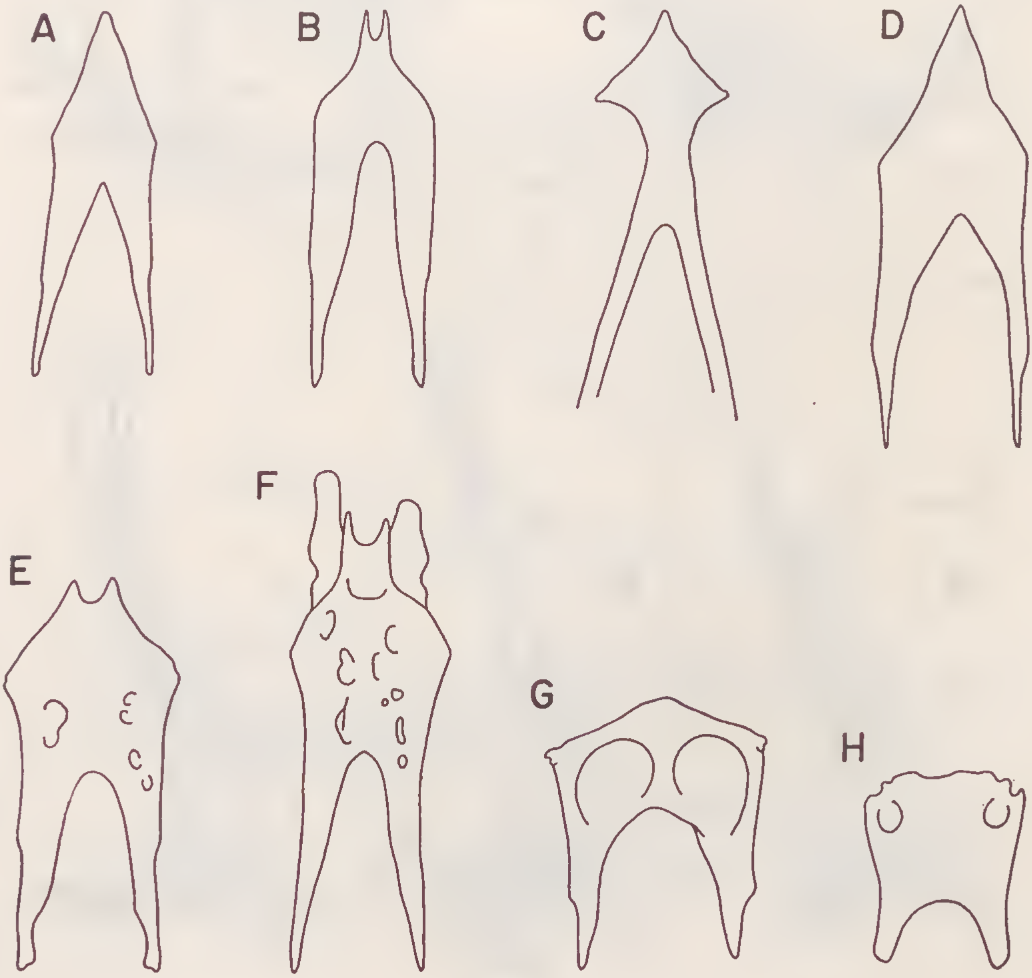

Fig. 7

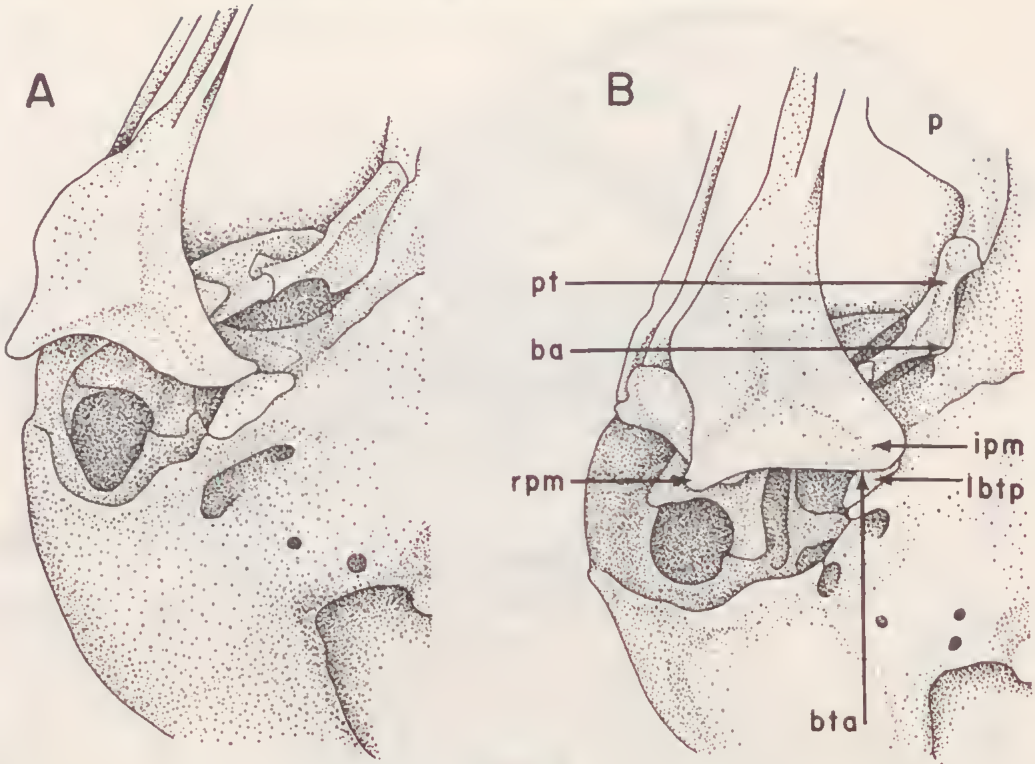

Fig. 8

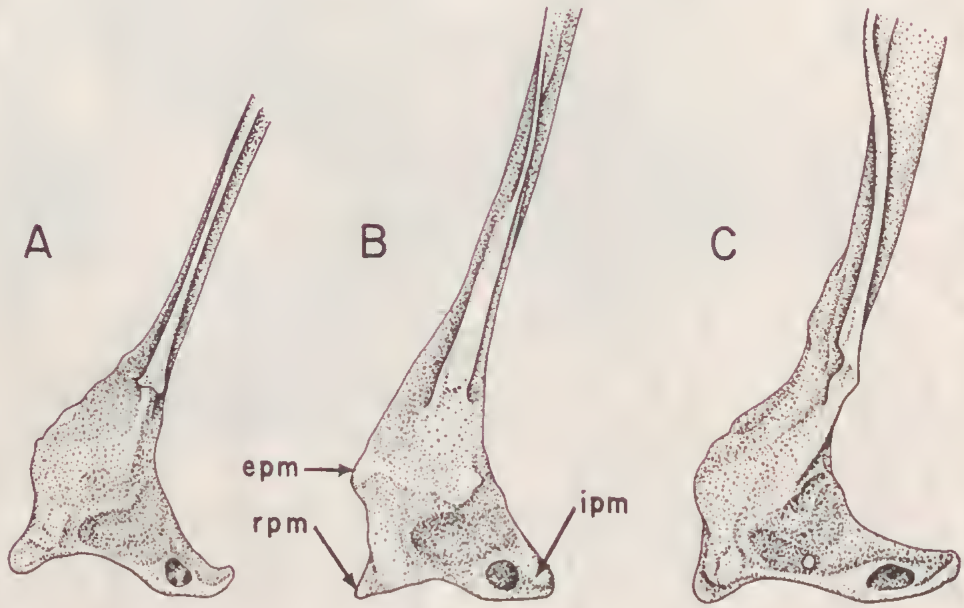

Fig. 9

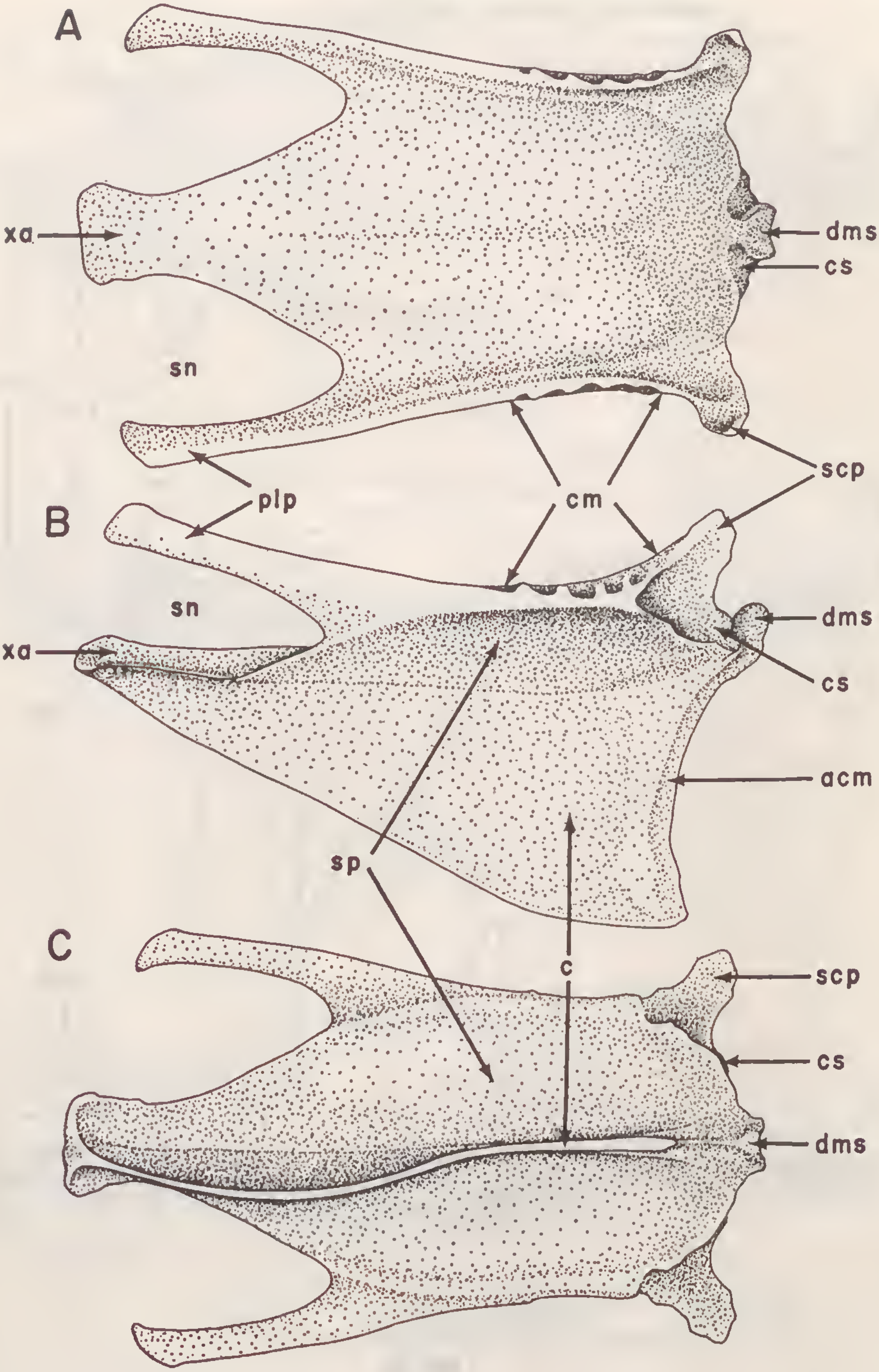

Fig. 10

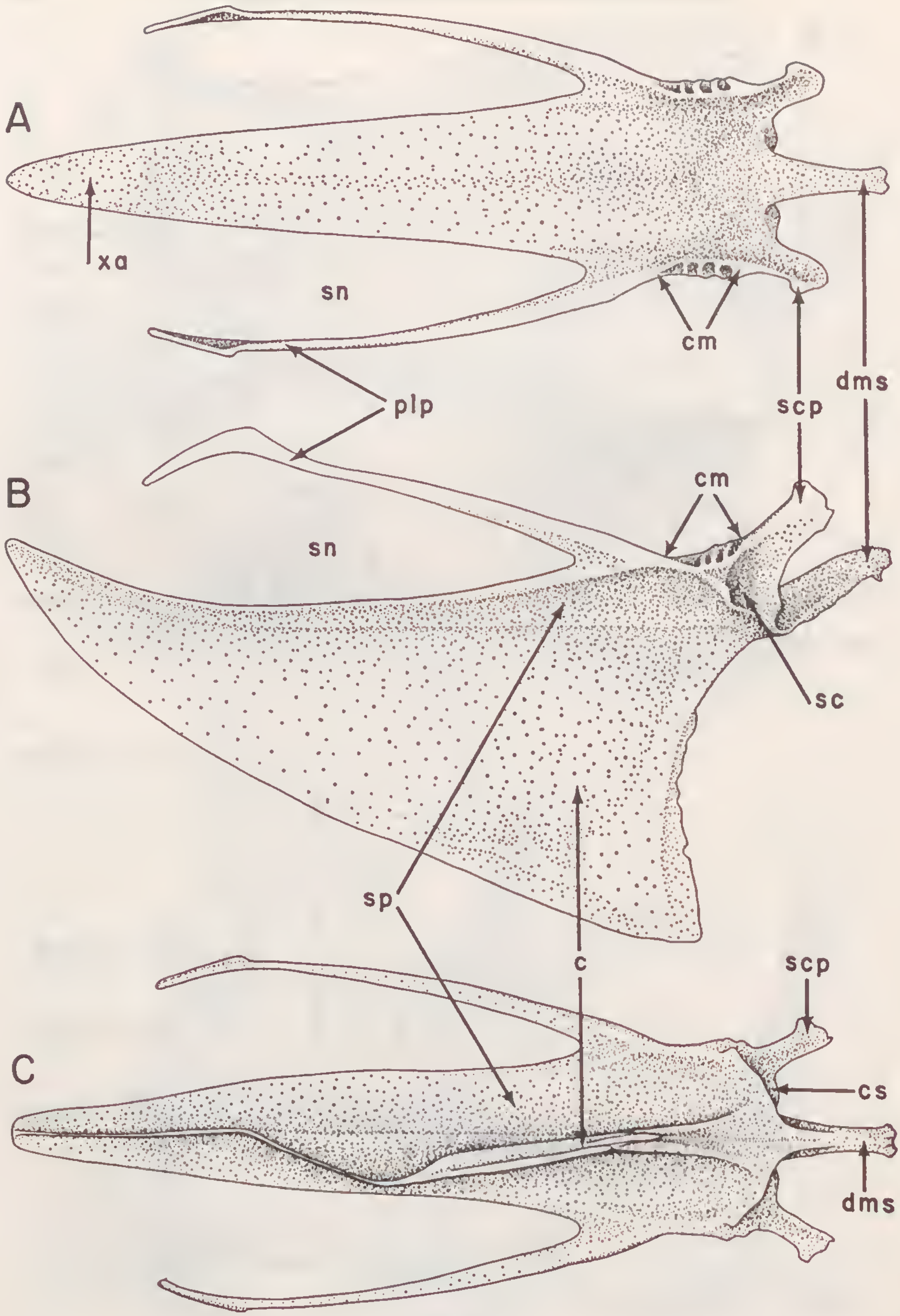

Fig. 11

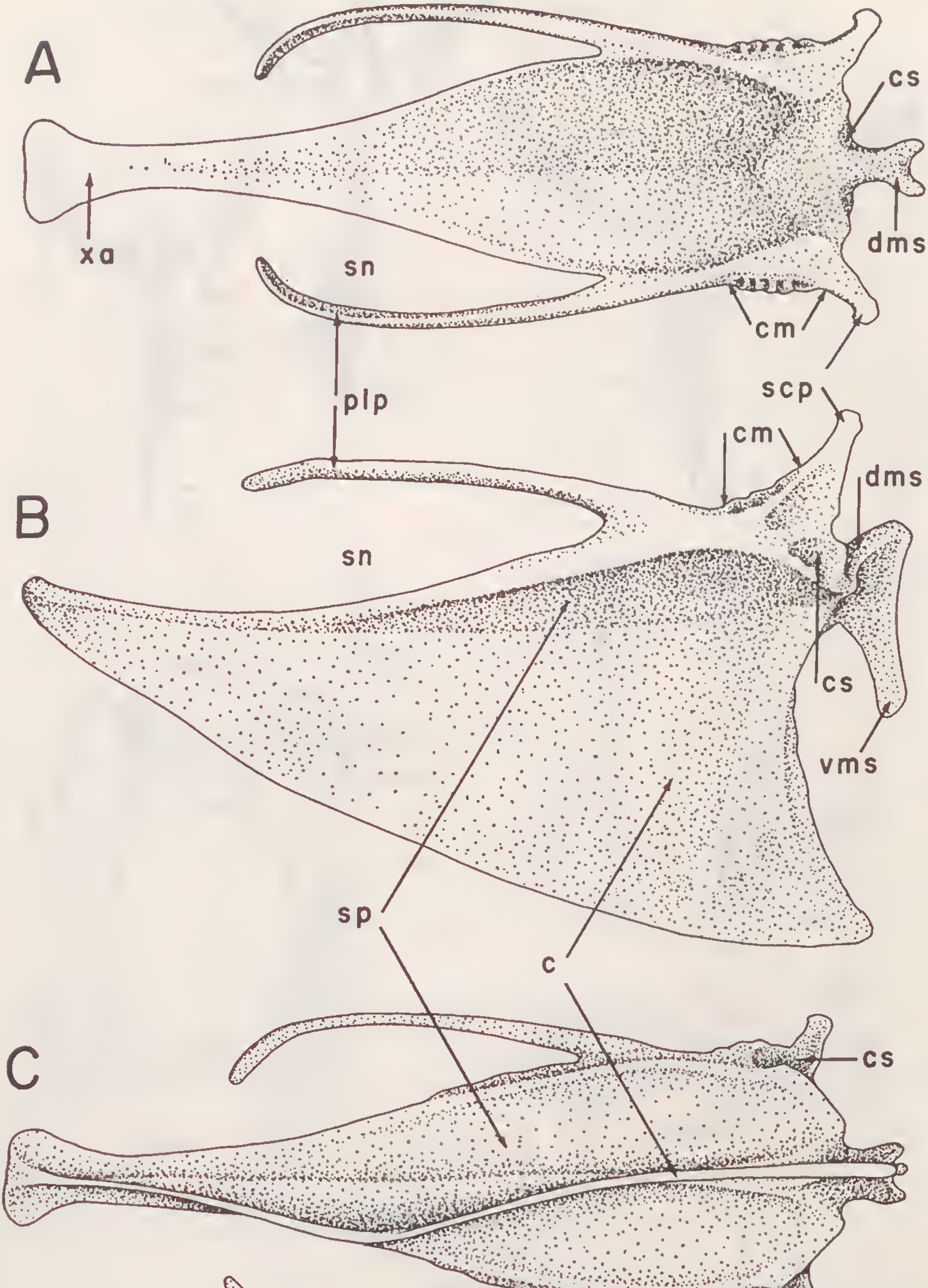

Fig. 12

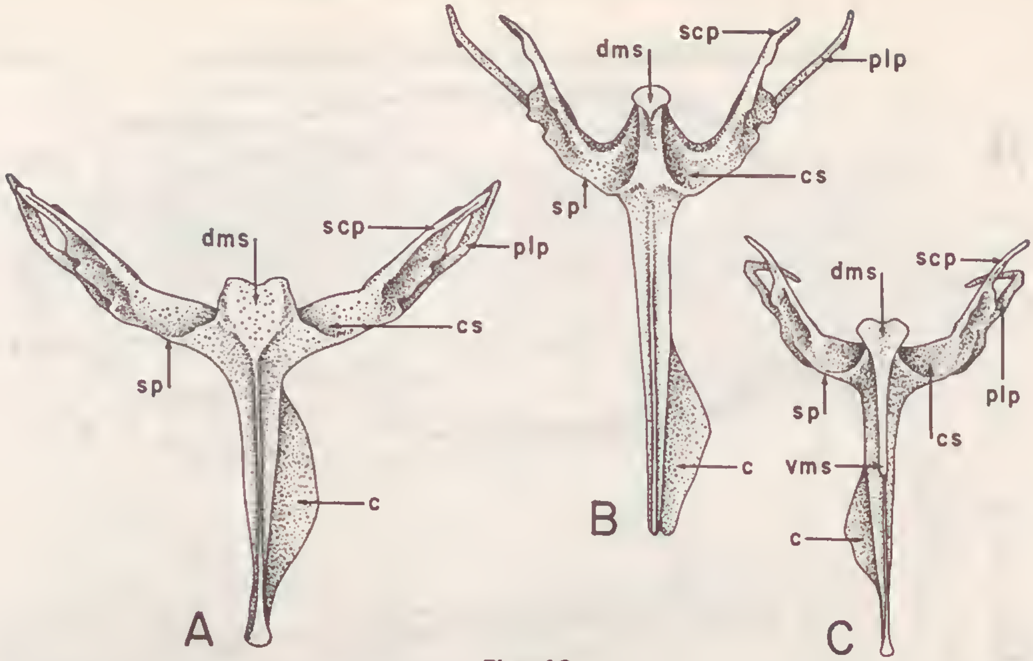
dms
scp
plp
cs
sp
c
A
B
vms
C

Fig. 13

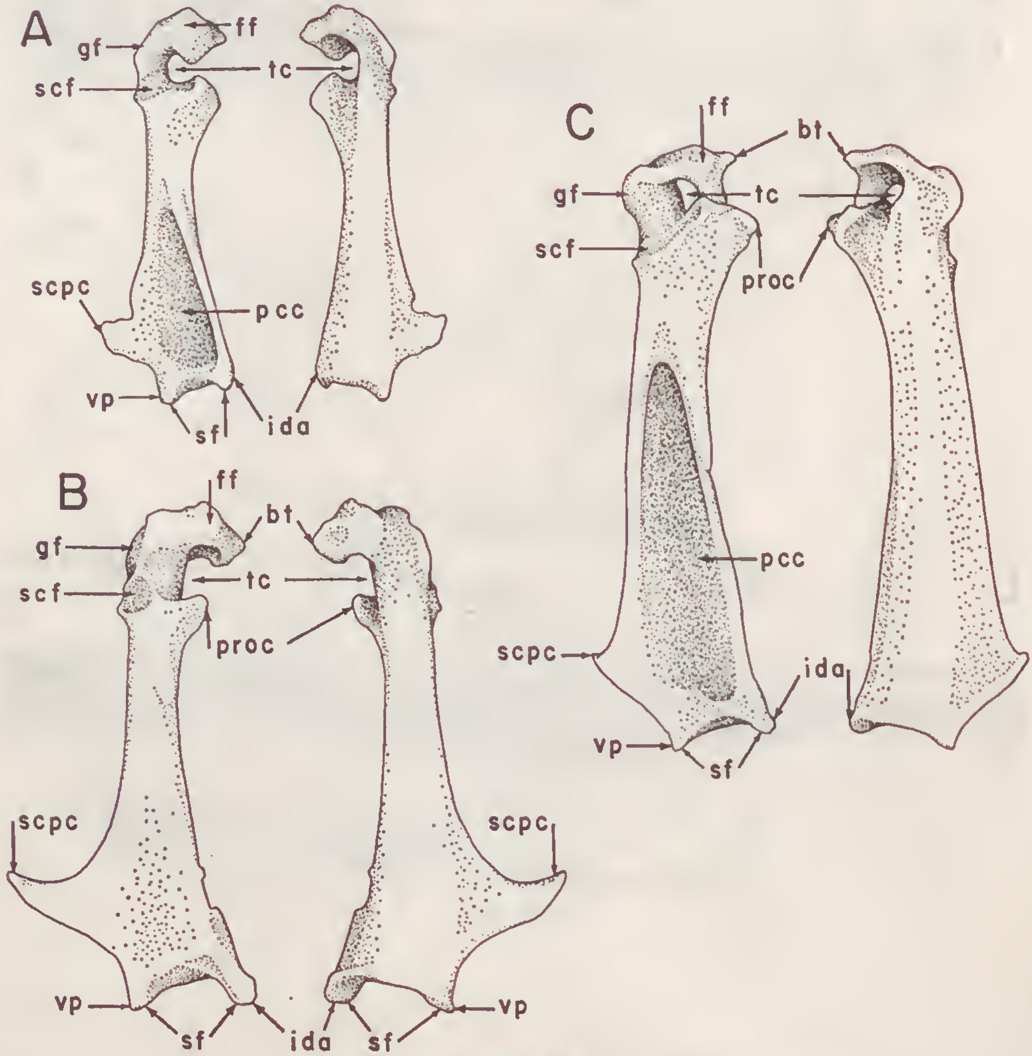
A
ff
gf
tc
scf
scpc
pcc
vp
sf
ida
B
bt
proc
C

Fig. 14

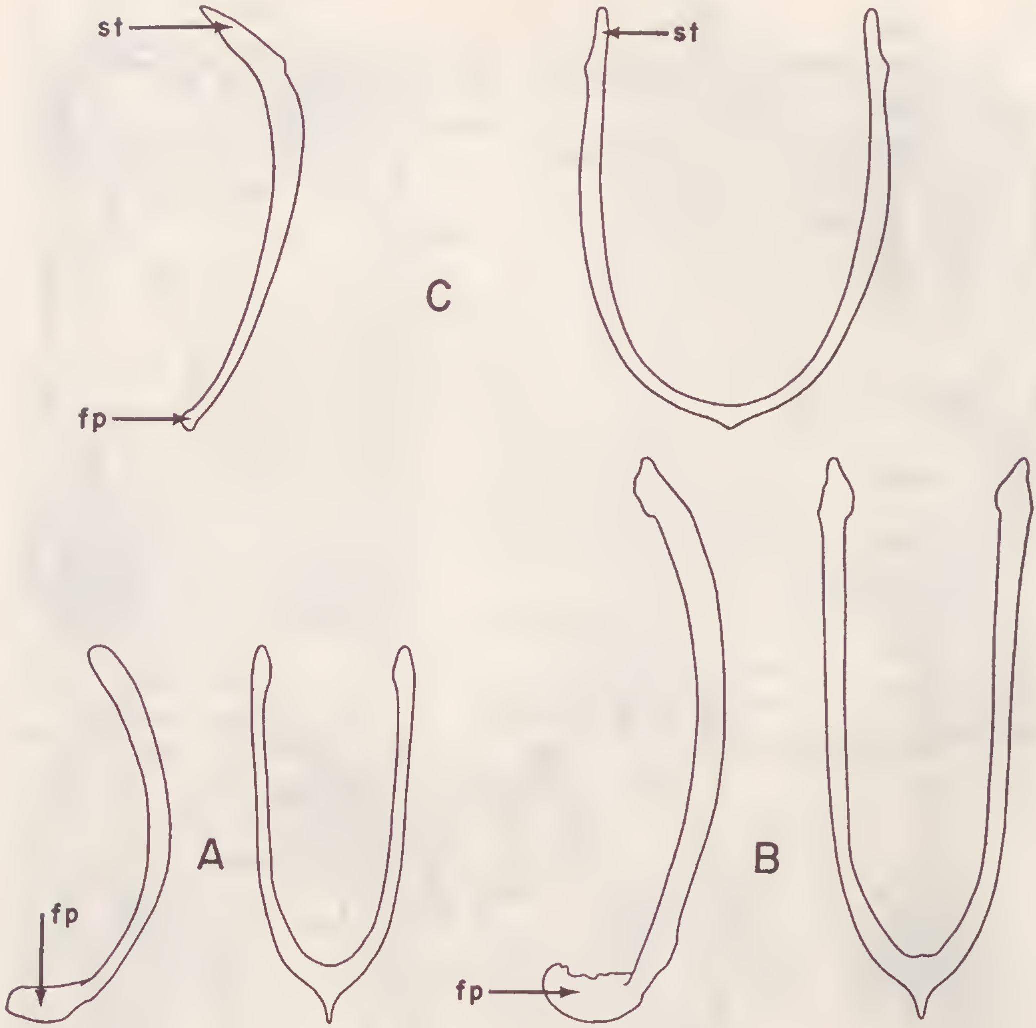

Fig. 15

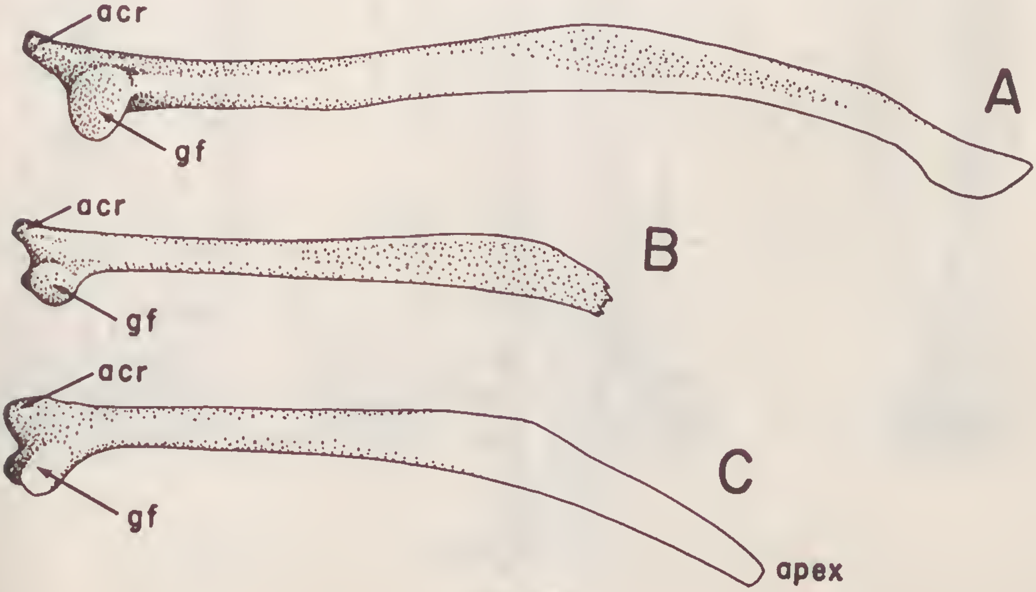

Fig. 16

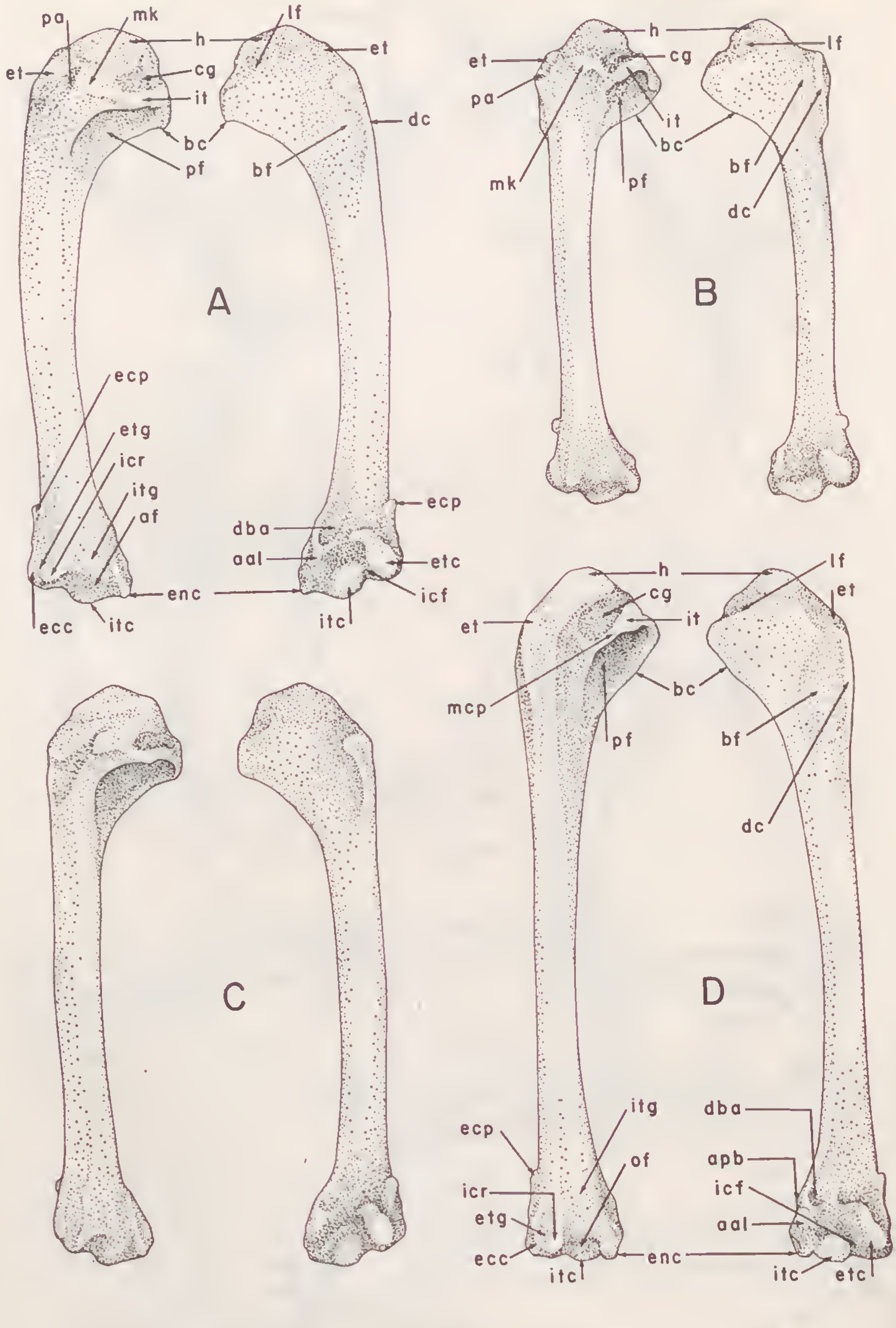
A
B
C
D
pa
mk
lf
h
et
cg
it
bc
pf
bf
dc
ecp
etg
icr
itg
af
dba
aal
etc
icf
enc
ecc
itc
mcp
of
apb

Fig. 17

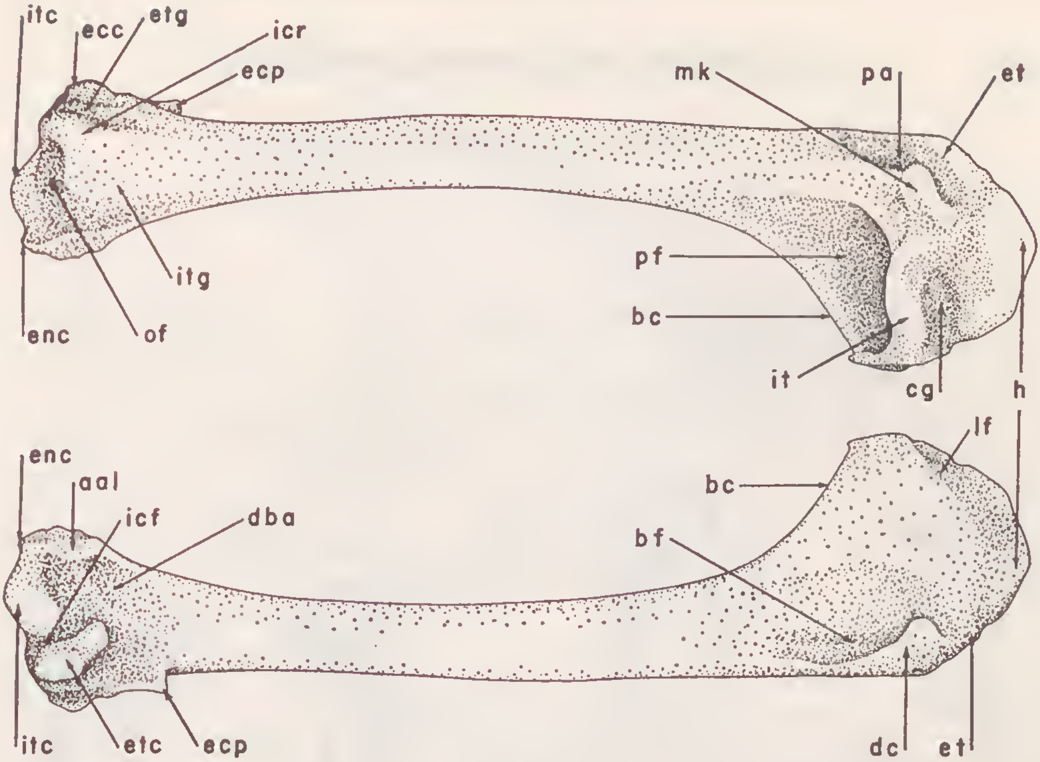
itc
ecc
etg
icr
ecp
mk
pa
et
pf
bc
it
cg
h
itg
enc
of
enc
aal
icf
dba
lf
bc
bf
itc
etc
ecp
dc
et

Fig. 18

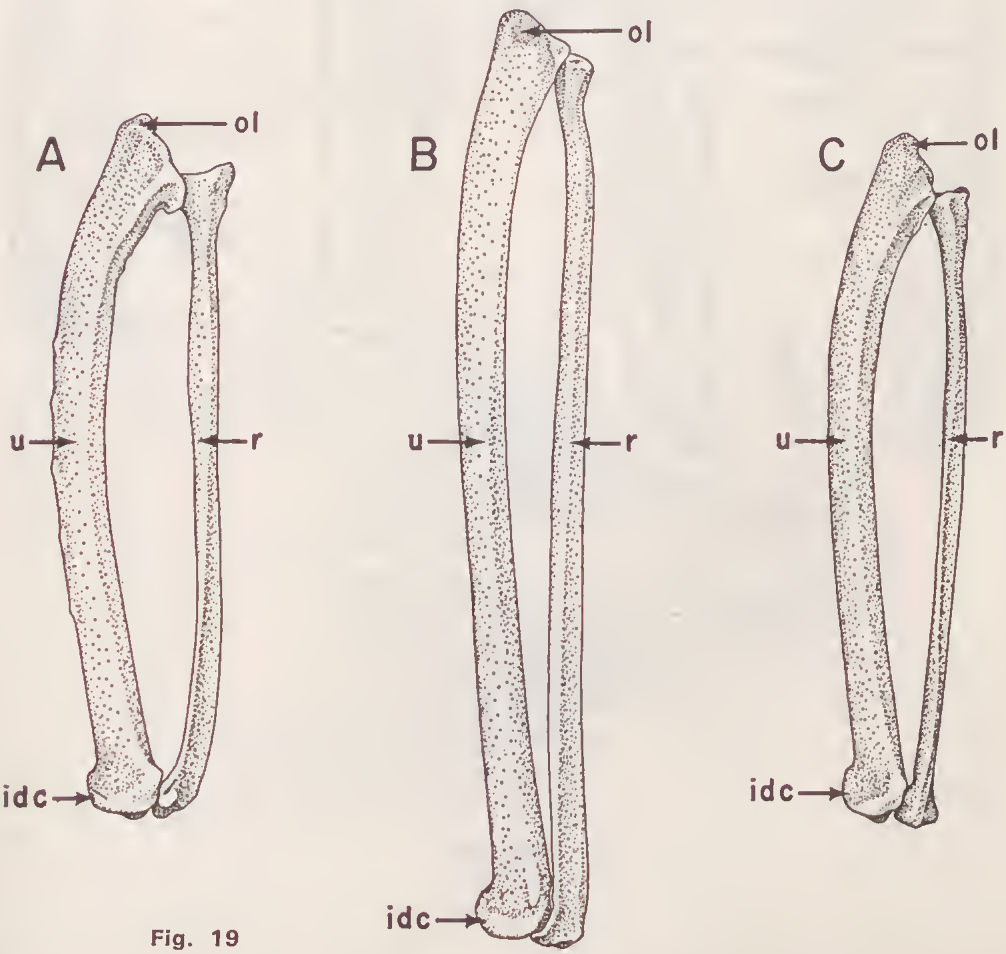
A
B
C
ol
ol
ol
u
r
u
r
u
r
idc
idc
idc

Fig. 19

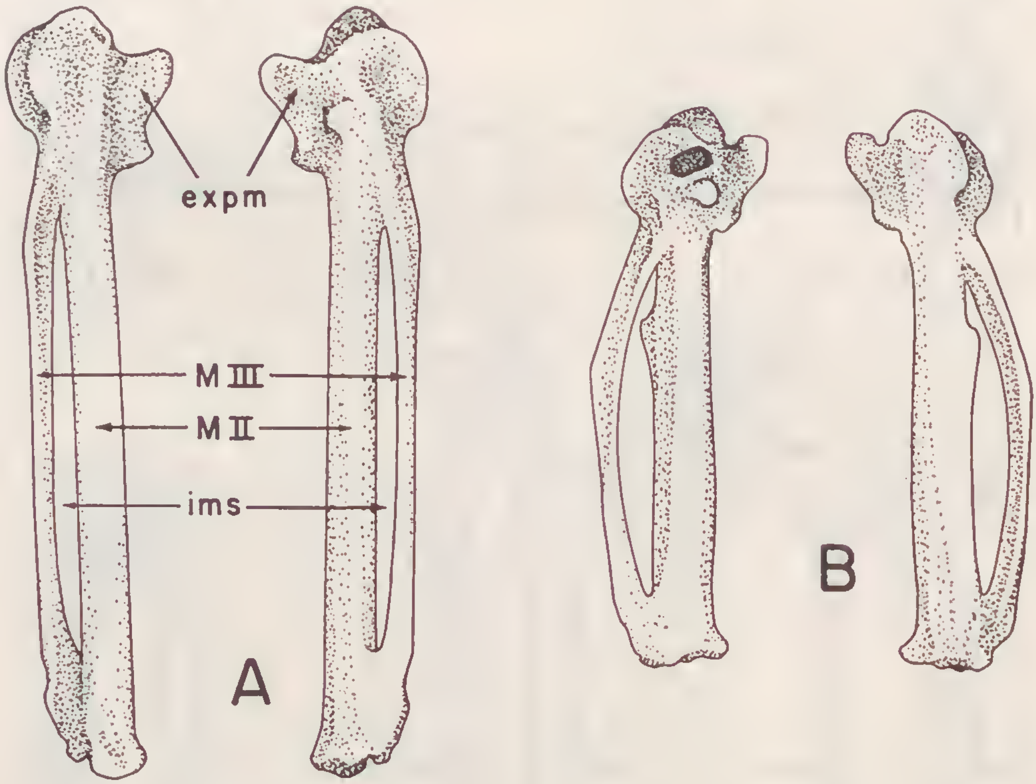

Fig. 20

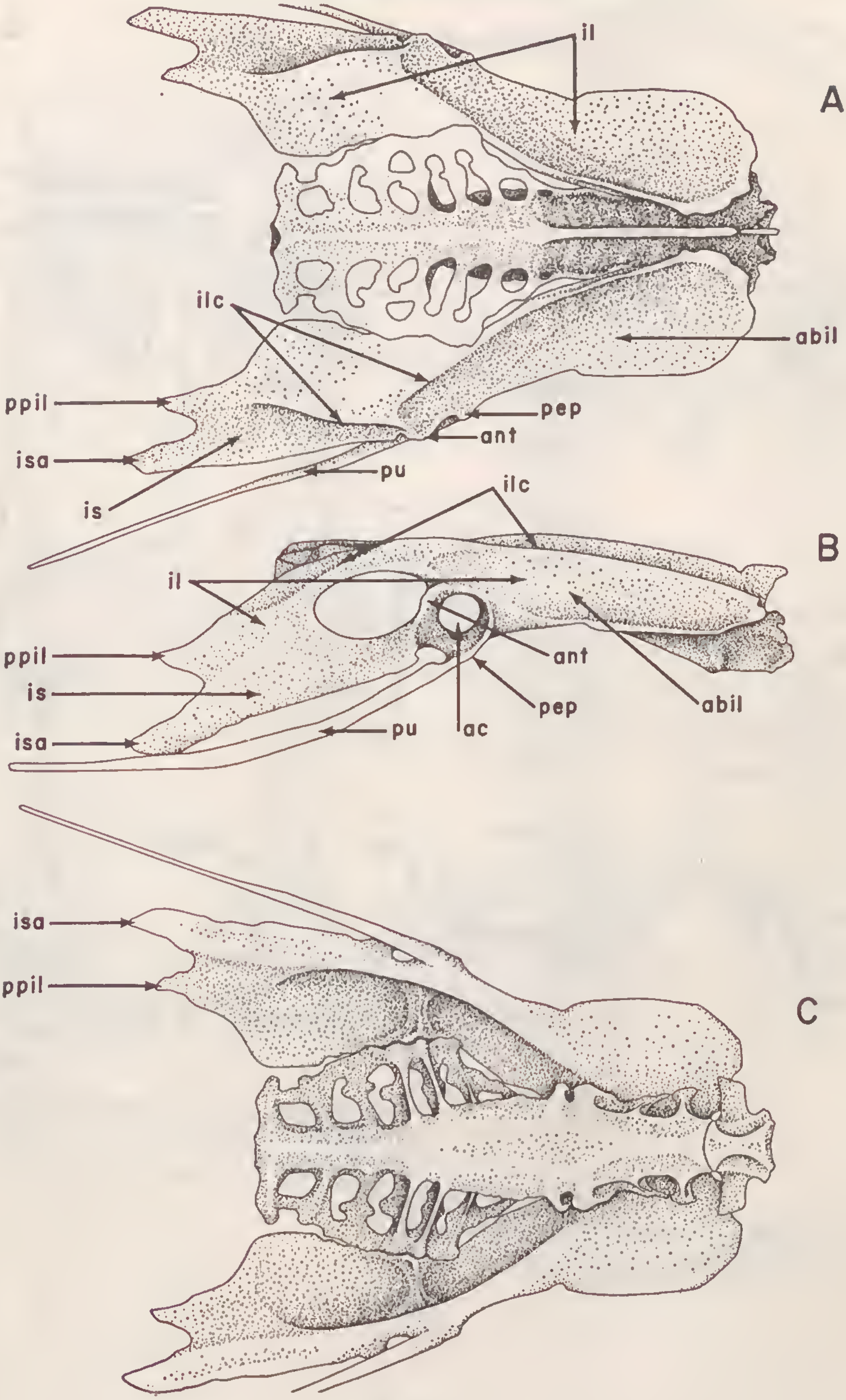
il
A
abil
ilc
ppil
pep
ant
isa
pu
is
ilc
B
il
ant
ppil
is
pep
abil
isa
pu
ac
isa
ppil
C

Fig. 21

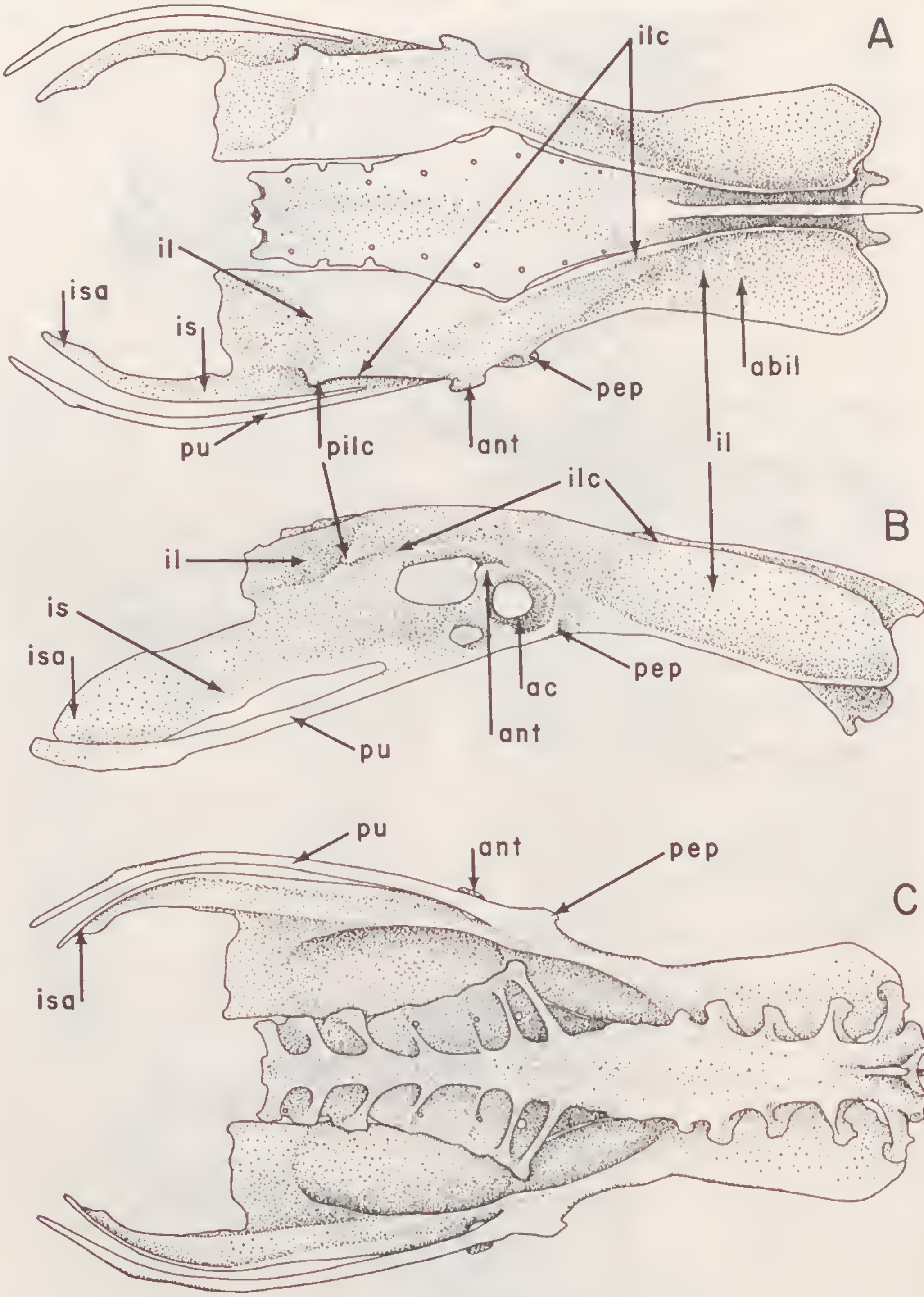
A
ilc
il
isa
is
abil
pep
pu
pilc
ant
il
B
ilc
il
is
isa
pep
ac
ant
pu
C
pu
ant
pep
isa

Fig. 22

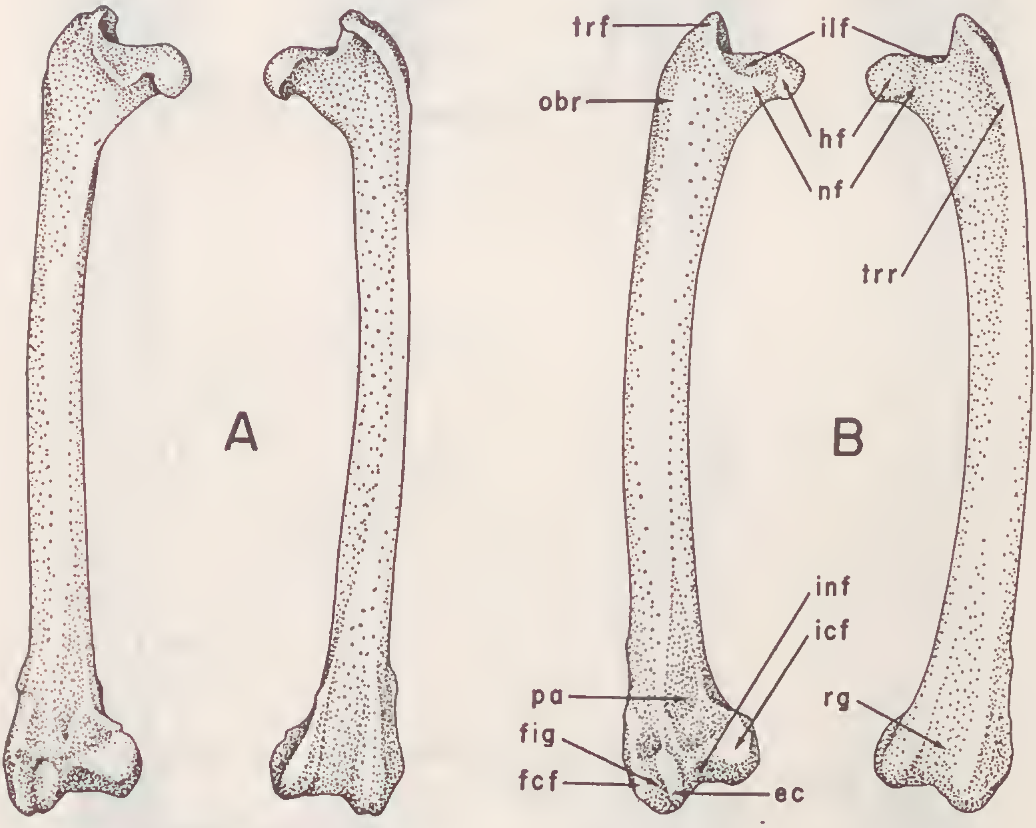

Fig. 23

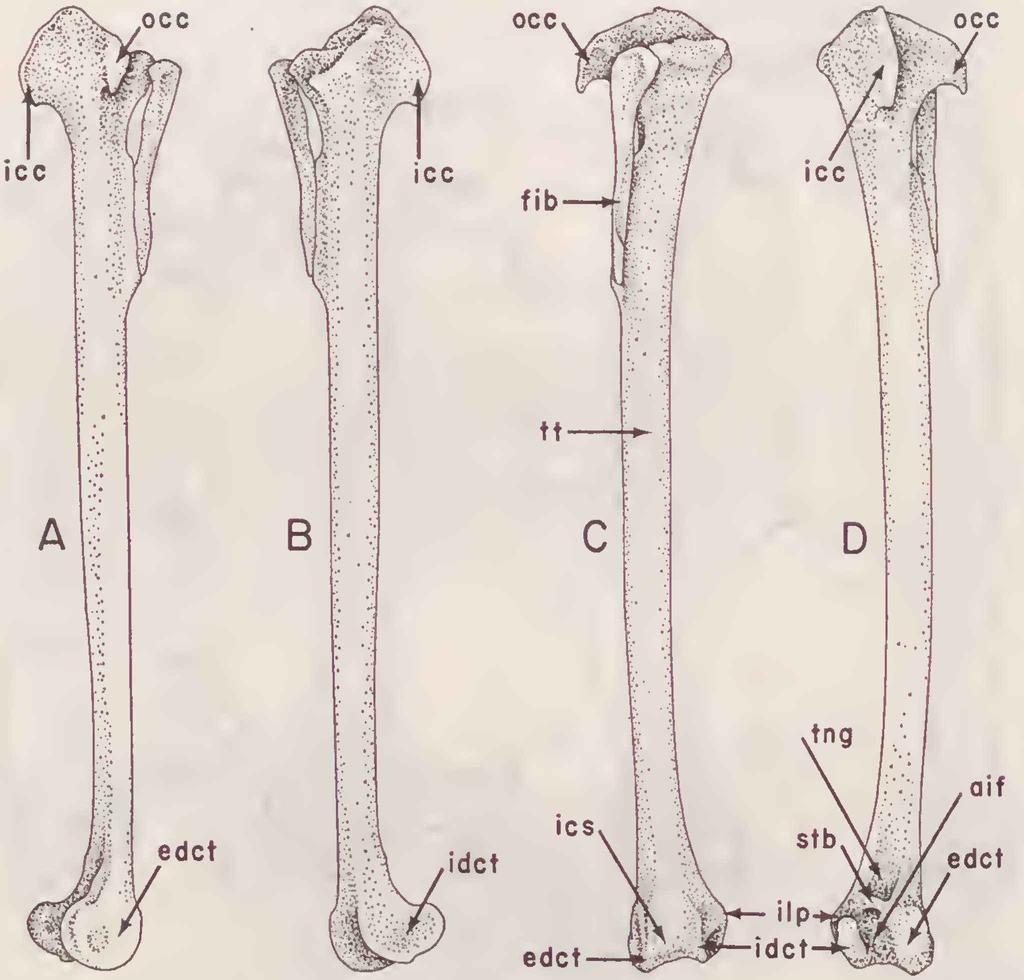
occ
icc
A
icc
B
occ
fib
tt
C
ics
edct
ilp
idct
occ
icc
D
tng
aif
stb
edct
edct
idct
ilp
idct

Fig. 24

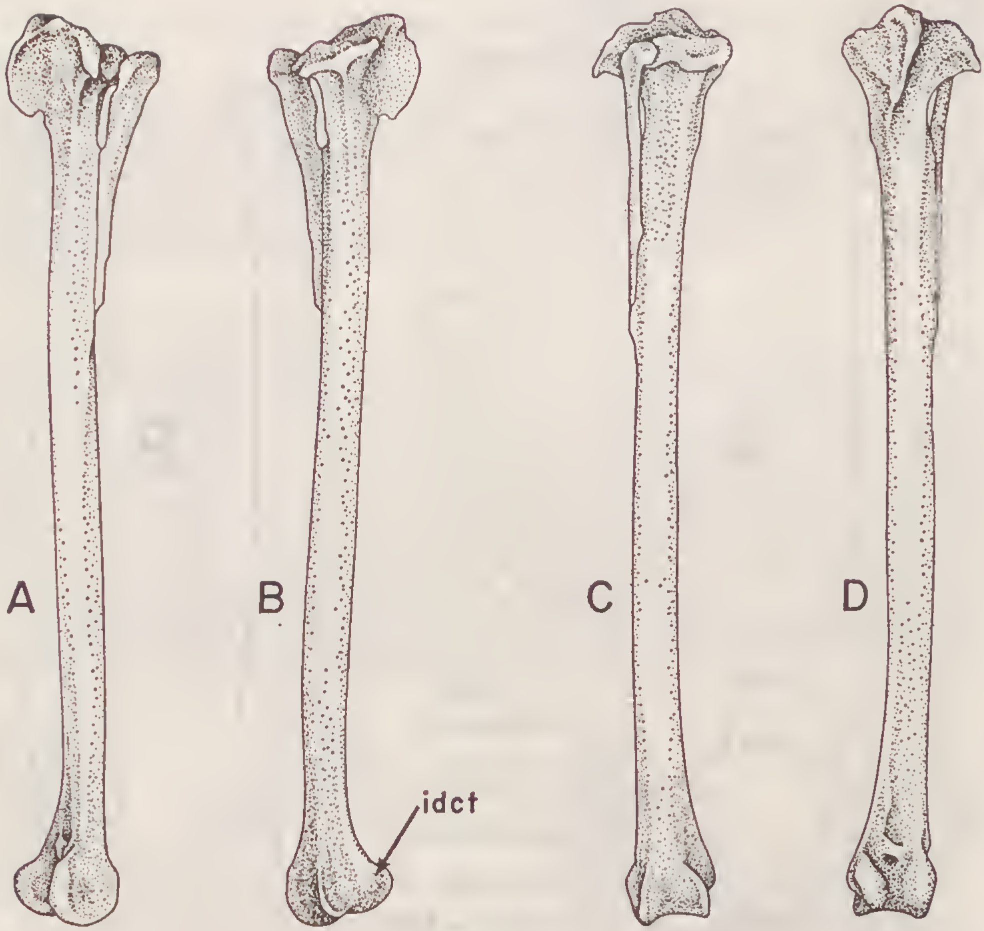

Fig. 25

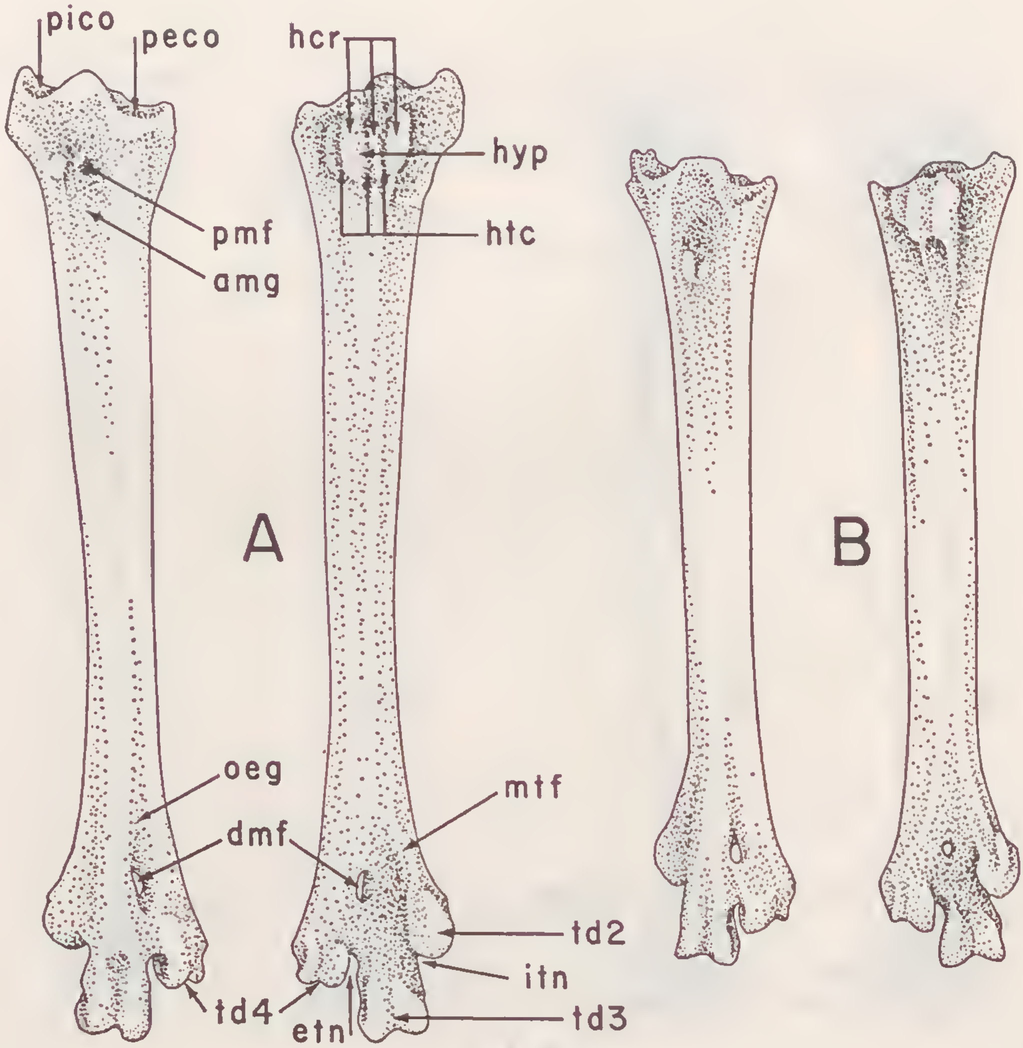

Fig. 26